STUDIES ON THE MECHANISMS OF VISION

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VOLUME I

WORKS SUBMITTED FOR THE DEGREE OF

DOCTOR OF SCIENCE

UNIVERSITY OF EDINBURGH

1982

DEDICATED WITH GRATITUDE TO

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AND

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VOLUME I

ABSTRACT

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These works treat comparative anatomical and physiological aspects of visual information processing. An extensive introductory review surveys the relationship between the design of the mammalian eye and the life style in which it is employed.

Subsequent less general studies deal with topics ranging from schematic eyes, the refractive state of the eye, the organisation of the retinal ganglion cell layer and optic nerve, the variety of retinal ganglion cell distribution, species differences in ganglion cell receptive field properties, to eye movements and the organisation of primary visual cortex.

Outcomes of this work include the development of a schematic eye which incorporates a gradient index lens, an extended analysis of profiles in the retinal ganglion cell layer which has led to the identification of *large* populations of displaced amacrine cells in the mammalian retina, a correlation between the physiology and anatomy of cat retinal ganglion cells based upon application of sampling theory, the first demonstration of version in rabbit and of vergence in a subprimate and a reinterpretation of binocular organisation in rabbit primary visual cortex.

EXPOSITION

EXPOSITION

Sturmius held, that the examination of the eye was a cure for atheism. Besides that conformity to optical principles which its internal constitution displays, and which alone amounts to a manifestation of intelligence having been exerted in its structure; besides this, which forms, no doubt, the leading character of the organ, there is to be seen, in everything belonging to it and about it, an extraordinary degree of care, an anxiety for its preservation, due, if we may so speak, to its value and tenderness.

William Paley, Natural Theology 1836.

According to the bent of an investigator, comparative study of the eye's adaptation to a variety of life styles and habitats provides plentiful evidence for the operation of intelligence or natural selection! The optics of nocturnal and diurnal species differ in functionally explicable ways, the relative population of rod and cone receptors varies as the time spent by a species in activity at different light intensities, photoreceptor pigments may be often shown to be matched to the spectral environment and the variety of retinal ganglion cell topographic distributions, including fish with *two* visual streaks in each eye (p.103), can be correlated with the range of behavioural patterns and environments occupied by their possessors.

Some apparently elementary aspects of ocular adaptation, such as the variety of pupil shape in different species, remain unsystematised. At first thought, it would be expected that the application of optical theory would provide automatic insight into the potential role of such variation. However, the role of the pupil form may only be comprehensible against a background of analytic understanding of the systems design of the eye, the strategies that it employs to attain high acuity under different conditions of light intensity, motion sensitivity or

matching between optical and neural image quality across the retina.

We may be able to come readily to grips with some aspects of ocular design, its adaptations to increase quantum capture, or attain colour vision without compromising other performances. However, in most areas it is necessary to accept that the eye is not an organ subject to pressure to optimise a single function. It has to compromise between possibly conflicting demands. Many of these may be very subtle. In certain small animals the factors tending to induce increase in eye size may be in direct conflict with those leading towards an increase in brain size because of competition for space. General principles determining the eye size may then be obscured. Similarly the variation in total optic nerve count between species might be strongly influenced by competition between different sensory modalities for telencephalic representation, thus obscuring any patterns arising from more readily quantified influences.

Whether it is intended to develop an analytic understanding of some theoretically accessible component of ocular organisation or to tackle some of the more grandiose problems, such as the functional reasons underlying the development of frontality, the investigator is faced with the same difficulty. A lack of reliable, quantitative, comparative data. Even the extent of the visual field of the domestic cat has been overestimated until recently by some 90° (p.182). What reliance can therefore be placed on data from rare species which may be pivotal to some generalisation?

The first contribution to this thematic collection (*Hughes, 1977, The topography of vision in mammals of contrasting life style.; p.* 1) undertakes a synthetic and critical comparative review of factors determining

the quality of vision across the visual field. Its aim is to indicate some of the broader open-questions and to encourage aquisition of the more mundane facts required before work of synthesis can hope to succeed. Looking back at the rapidly accumulating comparative literature of the past five or six years it is apparent that the article reflected, rather than anticipated, the recent upsurge in emphasis on comparative visual physiology.

OPTICS

The whole topic of physiological optics is a good example of a field ripe for synthetic and comparative development. The work of acquiring routine data on eye organisation for a variety of species (*Hughes, 1979, A schematic eye for the rat.; p.* 145*: Hughes, 1972, A schematic eye for the rabbit.; p.* 164*: Hughes, 1976, A supplement to the cat schematic eye.; p.* 182*: Hughes, 1979, A useful table of reduced schematic eyes... .; p.* 190) offset some gaps in the literature but also made me aware of the inadequacy of Gaussian schematic eyes for other than elementary purposes.

Of course, the development of more adequate models has long been hindered by the mathematical difficulties of an optical treatment for lenses containing a gradient of refractive index such as is found in the crystalline of the eye. A satisfactory theory for these lenses is, in fact, of quite recent origin and its general application is made possible only by the ready availability of digital computers. A recent collaboration between my laboratory and the Commonwealth Scientific and Industrial Research Organisation has been developing a model eye such that, given the paramaters of the original including the form of the refractive index distribution in the lens, it permits image quality to be predicted not only for the marginal rays

of finite pupil sizes but also for oblique imagery in the peripheral fundus. Given such a model, which is a physical description of the system not an arbitrary fit, it is possible to explore what happens to spherical aberration, astigmatism, coma and focus if certain parameters are slightly changed. Using such models the system design of the eye can be explored with previously unenvisaged ease in natural or artificial designs. Some overall view may be developed as to what is optimised in species with different types of eyes. Thus we may find that animals with a visual streak (p.92), or a visual axis well away from the optic axis, employ quite different strategies to determine their peripheral image quality when compared to those with a visual axis close to the optic axis.

The outcome of such analytic modelling may be confirmed by experiment. The first report on the use of the advanced eye model dealt with spherical aberrations for finite pupils (*Campbell and Hughes, 1981, An analytic gradient index schematic lens and eye for the rat... .; p.*193) and embodied experimental confirmation. The model has now been extended to deal with peripheral imagery and found satisfactory (*Campbell, Sands, Hughes, in preparation*). The programme developed by Sands for this work will shortly be freely available in the public domain in a user-interactive version so that non-mathematical physiologists will have a powerful tool for the design of sophisticated model eyes or for exploration of their properties at leisure.

Glickstein and Millodot made a major contribution in reviving the suggestion that the hypermetropia encountered during the refraction of small eyes is an artefact arising out of the use of reflections from the retinal surface rather than from the effective image shell. The set of papers on refraction (*Hughes,*

1977, The refractive state of the rat eye... .; p. 212: *Hughes and Vaney, 1979, The refractive state of the rabbit eye.; p.* 225: *Hughes, 1979, The artefact of retinoscopy in the rat.; p.*230) undertook to establish whether or not Glickstein and Millodot's theory was valid. The results clearly support their view.

An additional outcome of this work was the finding that the rabbit eye is free of oblique astigmatism out to 80° of eccentricity at least. This is a striking example of how the optics may be modulated to eliminate what would otherwise be a gross refractive aberration at large eccentricities in a system of concentric refracting surfaces and homogeneous lenses. The need for freedom from oblique astigmatism in the peripheral fundus is understandable in the rabbit which possesses an extensive visual streak.

Some authors have suggested the anterior field of the rabbit eye to be myopic for use in feeding. My own observations suggest emmetropia but a similar claim of myopia has been made for the lower anterior field of pigeons. It is not improbable that image focus differs across the representation of the visual field. It is envisaged that computer analysis of the rabbit and other eyes will reveal the basis of such variations in image quality and demonstrate variety in its topography from one species to another.

THE RETINAL GANGLION CELL LAYER

The optical apparatus sets bounds on the ultimate quality of the retinal image. The optic nerve, the 'bottleneck' of the visual system, determines its total channel capacity. But, so far, we have no insight into the reasons for the great variation between the optic nerve fibre counts of different species. However, as the final common path from the retina to the central nervous system, the number of optic nerve fibres originating from ganglion cells

in a given region of retina also determines the maximum possible neural resolution attainable for the corresponding patch of image. Density distribution maps of ganglion cells thus describe upper bounds on the distribution of resolution across the visual field.

The total optic nerve count is also a useful check on criteria employed for ganglion cell identification because integration of a ganglion cell distribution map should result in a similar total. That is, of course, if it is assumed that centrifugal fibres are rare and that branching does not occur in the optic nerve. However, the advent of axonally transported markers has reduced the importance of such means of confirming ganglion cell identification.

By 1977, optic nerve fibre counts had been carried out under the electron microscope with the advantage of similar methods for rat, rabbit and cat (*Hughes, 1977, The pigmented rat optic nerve... .; p.241 : Vaney and Hughes, 1976, The rabbit optic nerve... .; p.246: Hughes and Wässle, 1976, The cat optic nerve... .; p.257*). Counts of neurones presumed to be ganglion cells in the retinal ganglion cell layer were also available for rat, rabbit and cat (*Hughes, 1975, A quantitative analysis of the cat retinal ganglion cell topography.; p.271*).

Curiously, the population of presumed ganglion cells was twice the optic nerve count in rat, 40% greater in rabbit and about 20% greater in cat. Vaney therefore carried out a count of fibres entering and leaving small areas of rabbit retina and was able to compare the difference with the local cell count. This work revealed that the population of cell profiles identified as neurones by Nissl staining, and presumed to be ganglion cells, was made up of at least two morphologically distinct classes. The majority of classic neurones represented true ganglion cells and

were equal in number to the axons arising from that region of retina; most of the remaining cells were reminiscent of a crowned head in appearance and were called 'coronate' cells. Their total number sufficed to account for the difference between the rabbit optic nerve fibre total count and the presumed ganglion cell count.

The neuronal nature of the coronate cells was argued in detail (*Hughes and Vaney, 1980, Coronate cells: displaced amacrines of the rabbit retina?; p.293*) and, in contrast to Cajal's view, it was suggested for the first time that, in common with birds and reptiles, the mammals possess a large population of displaced amacrine cells in the ganglion cell layer. Not developmentally ectopic neurones, but cells there to do a specific job which has not so far been identified in modelling retinal function.

Definitive identification of coronate cells as amacrines requires staining of their processes and support from negative evidence; a consistent failure to demonstrate an axon-hillock or axon. This is reported by Vaney, Peichl and Boycott and from my laboratory (*Hughes and Wieniawa-Narkiewicz, in preparation*). In addition, it is necessary to make electron microscopic demonstration that the processes both give and receive synapses. It is then essential that the cell sectioned for the electron microscope is a coronate cell by light microscopic criteria and a technique was developed to ensure this (*Hughes and Wieniawa-Narkiewicz, 1982, A simple technique for the electron microscopy of retinal cells previously identified by Nissl staining and light microscopy.; p.358*). The results confirm the amacrine nature of the cells (in preparation).

A fresh look at cell profiles in the cat retina (*Hughes and wieniawa-Narkiewicz, 1980, A newly identified population of presumptive microneurones*

in the cat retinal ganglion cell layer.; p. 355) which employed kainic acid as a tool for identifying neurones, suggested the presence of very large numbers of tiny neurones in the ganglion cell layer - perhaps as many as 700,000. These cells had previously been identified as glia. Yet close inspection of lightly stained material revealed their morphology to be similar to that of the coronate cells which had originally (p.524) been identified in the rabbit as neurones and presumptive ganglion cells and not confused with glia. This discrepancy probably arose from the practice of staining cat retina with hot dyes after which the small neurones appear almost black, and resemble glial nuclei.

A detailed reexamination of the cat ganglion cell layer was then undertaken. It was additionally motivated by Stone and his colleagues' failure to confirm the above optic nerve fibre counts, ganglion cell total populations and peak counts at the area centralis etc. Advantage was taken in this work (*Hughes, 1981, Population magnitudes and distribution of the major modal classes of cat retinal ganglion cell.; p.293*) of the division of ganglion cell classes according to soma size by Boycott and Wässle, to map the modes of the cell classes separately (*Hughes, Caille, Vibert, 1980, A statistical analysis and comparison of doma diameter spectra for classical neurones... .; p.330*).

The outcome of this study is that the total classical neurone count, or presumed ganglion cell population, of the cat is some 210,000 neurones but of these no more than 170,000 appear to be ganglion cells. A class of larger cells which survive optic nerve section without retrograde degeneration was identified with distinctive features, including a nuclear bar, and were concluded to be another group

of displaced amacrine or association neurone distinct from the coronate types. The optic nerve population of 170-180,000 fibres is in good agreement with this ganglion cell count. Stone and his colleagues have recorded a maximum optic nerve fibre count of about 150,000 fibres or 88% of the value reported from my laboratory which is within the range of individual variation and error of method, although they also include markedly lower values. The peak ganglion cell count in the area centralis, an important value for defining the bounds on behavioural acuity in the cat, appears now to be generally accepted as some 9,000 g. cells/mm^2 in the adult as reported in 1975 (p.271).

The situation in the rat has been examined in other laboratories and the count of 118,000 fibres matched to that of retinal ganglion cells while the residuum of the 200,000 counted neurones in the rat ganglion cell layer appear to be displaced amacrines as in the rabbit and cat. Thus, in summary, the rabbit has about 400,000 ganglion cells, 150,000 coronate cells and possibly 30,000 other neurones in the ganglion cell layer. The cat has about 160-170,000 ganglion cells, 30-40,000 classic neurones which are probably interneurones or displaced amacrines, and perhaps as many as 700,000 microneurones representing various classes of displaced amacrine. The details of these classifications are being analysed at present with the combined light microscopy technique (p.358) in both rabbit and cat. The work is complemented by analysis of the process of retrograde retinal degeneration after optic nerve section. Our current work suggests the presence of some four classes of displaced amacrine cell in the rabbit retina. It remains for physiological investigations to take up the analysis of their possible roles.

GENERALISATIONS ON RETINAL ORGANISATION

The neurones of the retinal ganglion cell layer reveal a great variety of topographical distribution in different species. In a survey of mammalian retinas (p. 91) it was noted that two features were commonly encountered in their ganglion cell distribution, a visual streak extending across the retina parallel to the horizon and a circular area set at the region of retina receiving the image of the intersection of the median saggital plane and the horizon when the eyes are in the primary position. Theoretical models based on minimising sampling redundancy were put forward for these two distributions. The visual streak is related to the geometry of relatively open terrain and the circular area explained dynamically in terms of flow patterns about the destination point in the retinal image. These theories were based on a collection of over 200 retinal maps of which only a few have been published (p. 92). The thesis was first crudely presented in a paper on the retinas of kangaroos (*Hughes, 1974, A comparison of retinal ganglion cell topography in the plains and tree kangaroo.; p.370*). Some aspects of the 'terrain' theory are commonly misunderstood and these are taken up along with the problems which face it in a recent letter (*Hughes, A, 1981, One brush tailed possum can browse as much pasture as 0.06 sheep... .; p.372*).

A more specific application of sampling theory became possible upon the mapping of the approximate β-mode of the retinal ganglion cell density distribution (p.293). These cells are thought to correspond to the brisk-sustained units encountered during physiological studies of the cat ganglion cell receptive fields and to be the basis for high resolution vision in this animal. For the first time it was thus possible to apply the sampling theorem to the anatomical distribution of ganglion cells and

predict the highest resolvable grating frequency at various retinal eccentricities. For one model these predictions well match the physiological observations of Cleland. A similar analysis for the α-cells, or brisk-transient units, did not indicate a system organised in accord with optimal sampling theory.

Twenty years ago Maturana suggested that vertebrates might be divided into those which lacked a neocortex but possessed retinas containing non-concentric receptive fields which pre-analysed the image and thus reduced the central analytic load with the loss of flexibility in central analysis, and those possessing a neocortex served by a retina equipped only with concentric units which delayed image processing until a later stage and retained flexibility. This hypothesis is discussed at various points below (p.393 , 410 , 592 , 625) but was swiftly shown to be invalid. A series of *ad hoc* adjustments have survived equally poorly and we currently lack an overall synthetic view of the functional reasons for the existence of the variety of receptive fields and whether species differ significantly in the range they possess.

A major problem is that reliable data on the presence or absence of receptive field types is gained only from large samples of units recorded by the little practised and difficult intra ocular technique. Recording from the optic nerve emphasises larger fibers and can lead to a failure to observe cell classes. Even so, the latter method successfully demonstrates the presence of directional units in rat, contrary to previous reports, and goat (*Hughes, 1980, Directional units in the rat optic nerve.; p.388 : Hughes and Whitteridge, 1973, The receptive fields and topographical distribution of goat retinal ganglion cells.; p.374*).

More recently, the retina of the marsupial Tammar Wallaby was explored in detail by intraocular recording

(*Hughes and Slater, 1982, Some comparative and evolutionary reflections arising out of studies on retinal coding in the wallaby.; p.393*). Nearly all major classes of receptive field found in cat or rabbit were encountered in the wallaby. These results have been a great stimulus to my comparative thinking about this problem and work is underway to determine the extent to which retinal-unit receptive field varieties are universal throughout the vertebrate range.

I must confess, like T.H. Huxley, to find polemic as little abhorrent 'as gin to a reclaimed drunkard'. The diversion into the philosophy of nomenclature in unit studies (*Hughes, 1978, A rose by any other name. On 'naming of neurones'.; p.394*) and the reply to it were invigorating to the protagonists (although reader's responses were varied, ranging from 'very poor taste' upwards). However, the reply to my comments was unsatisfying and I wrote a further critique; by the time it was complete the issue appeared to have resolved itself with a movement away from the use of 'W' nomenclature. The manuscript was put aside unpublished. I include it here for completeness (p.407) although, of course, it unfortunately lacks a reply.

EYE MOVEMENTS

Extraordinary as it may now seem, it was generally believed until the beginning of the 70's that subprimate mammals do not verge their eyes. Indeed, work on the optic was almost non-existent. Although difficulties were encountered, the study on cat vergence (*Hughes, 1972, Vergence in the cat.; p.434*) established the ability of the animal to verge. Every cat I now encounter seems to do it! However, I could not detect vergence in rats (unpublished; but I am sure they can) or rabbits (p.561). More recently, however, Collewijn has shown the rabbit to possess well developed

vergence movements. Things have changed somewhat since 1971 when even a report of voluntary version movements of the rabbit eye (p. 558) elicited heated debate at the Rotterdam Symposium!

VISUAL CORTEX

In the past, the rabbit (p.122) has often been contrasted with the cat and its visual system suggested to be organised in quite different fashion on the weakest evidence. Many of these differences have been shown to be false, rabbits do not lack a binocular visual field, they can carry out version and vergence movements of their eyes, both cats and rabbits have a visual streak and the receptive fields of their retinal ganglion cells have very similar physiological properties.

The limited amount of work carried out on the central visual mechanisms of rabbits has restricted their close comparison with cat but again striking differences have been claimed by some authors. Perhaps one of the most bizarre claims of difference was the tacit acceptance in the literature that the 25° receptive field disparities of rabbit binocular units in primary visual cortex were probably not removed in normal activity and that the cells, would, therefore, never be subject to binocular stimulation by a real object. Investigation of this curious arrangement (*Hughes and Vaney, 1982, The organisation of binocular cortex in the primary visual area of the rabbit.; p.* 469) revealed a striking 'two-state' visual system in the rabbit which requires much further investigation if its ramifications are to be followed-through and its possible analogs identified in other species.

This work on rabbit binocular cortex permitted examination of its receptive field organisation (*Vaney and Hughes, 1982, Single unit receptive fields in the rabbit primary binocular cortex.; p.* 483). They were

found to be similar to those of monocular rabbit cortex. The high percentage of non-orientation selective units distinguishes it from cat primary binocular cortex but the possibility remains that such cells have not yet been encountered in the cat because of electrode selectivity. After all, the cat lateral geniculate nucleus contains the projection of nearly all classes of sluggish and rarely encountered receptive fields and these do,in turn,project to primary visual cortex. Are their receptive field properties so compounded upon arrival at the cortex as to make them unindentifiable? In the rabbit, such a hypothesis would appear to be invalid. Most of the retinal receptive field classes can be recognised in little changed form amongst the wide variety of encountered cortical units. Perhaps these non-concentric units simply project to small, rarely encountered cells in cat cortex.

PROLEGOMENA

The last work in this collection is chronologically one of the earliest (*Hughes, 1971, Topographical relationships between the anatomy and physiology of the rabbit visual system.; p.* 511). It attempted to consider the entire visual system of the rabbit, from its optics to the functioning of its visual cortex, in the light of the animal's life style and habitat. Experiments were carried out to plug the gaps where information was lacking. It now stands as a prolegomena to a similar treatment of the entire vertebrate group which will be in part based on the material presented below.

VISUAL ECOLOGY

A SURVEY OF THEMES

Chapter 11

The Topography of Vision in Mammals of Contrasting Life Style: Comparative Optics and Retinal Organisation

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With 26 Figures

Contents

Glossary of Abbreviations

CMF	Cortical magnification factor, mm/°
CNS	Central nervous system
CSF	Contrast sensitivity function
LSF	Line spread function
MTF	Modulation transfer function
PND	Posterior nodal distance, mm
PSF	Point spread function
RMF	Retinal magnification factor, mm/°

> The physiologist, who is conversant with natural history in general, is fortified against uncertain opinions, and the showy but flimsy textures of verbal sophistry. An hypothesis, which to others appears perfectly adequate to the object in view, is not convincing to him. He rises above the particular object to which it is accommodated, in order to appreciate its value; as we ascend an eminence to gain a commanding view of a district ...
>
> The basis of our physiological principles is rendered broader and deeper, in proportion as our survey of living beings is more extensive ... These enlarged views, which unfold to us the natural play of the animal mechanism, are our surest guide in the study of its deranged motions, an essential criterion for estimating the nature and degree of the deviation, and an important indication of the means by which it may be corrected

> ... On such researches, and such studies, on a foundation no less extensive than the whole empire of living nature, the science of medicine must be established; if indeed, it is destined to occupy the rank of a science.
>
> LAWRENCE: Lectures on Comparative Anatomy, Physiology, Zoology and the Natural History of Man, 1844, London.

A. Introduction

> The eye to this day gives me a cold shudder

wrote DARWIN (1860),

> to suppose that the eye with all its inimitable contrivances ... could have been formed by natural selection, seems, I freely confess, absurd in the highest degree.

but

> when I think of the fine known gradations, my reason tells me I ought to conquer the cold shudder.

Our knowledge of these gradations and the great variety of ocular organisation has been summarised in several large works in the last four decades (FRANZ, 1934; WALLS, 1942; ROCHON-DUVIGNEAUD, 1943; POLYAK, 1957; DUKE-ELDER, 1958). Of these authors perhaps WALLS (1942) has done most to emphasize and stimulate interest in, the extreme evolutionary adaptive lability of the eye. His book has served for some 30 years as a compendium of visual anatomy and physiology; although an essential reference, because unequalled in scope, many of its sections contain much that is misleading according to the current consensus. What appear in isolation to be relatively unimportant errors, such as

> where the eyes are placed laterally as in the rabbit, there is usually no area centralis ... and there are no spontaneous movements at all ...
> no non-simian mammal can converge its eyes ...
> among the carnivores, the domestic cat is pre-eminent with ... a binocular field of 130° and a total field of 287° ...

are quite common and may suggest to the reader outmoded qualitative distinctions between species, and further the erroneous generalisations which are so common in comparative literature.

In spite of the vast increase in comparative visual information since the appearance of WALLS' book, it remains difficult to make a quantitative comparative survey of even relatively straightforward problems, such as the extent of the visual field, because of the dearth of reliable data for not only *ferae naturae* but also the common laboratory animals. The situation is improving, but much systematic "bread-and-butter" work remains which might readily be undertaken with the armamentarium of the most underpriviliged laboratories of these stringent times. However, such work can be tedious and certainly lacks the charisma of the in-

vogue, front-line topics; the information backlog must be reduced in a process of attrition by a very limited number of comparatively orientated physiologists and anatomists.

Revision of WALLS' book in its entirety would now be a formidable task in which much of its idiosyncratic flavor and breadth of insight could be lost; the aim of this chapter is much more modest. It deals with some of the topics of WALLS' Chapter 10, "Adaptations to Space and Motion," in a modern context and is primarily concerned with the mammals. The topics subsequently dealt with may appear to be selected rather arbitrarily, but their common thread is that they are factors which set limits on the extent and quality of the spatial contrast information which a given species may acquire from its environment; little attention is given to the mechanisms for its analysis.

I. The Theme: Some General Observations on the Relationship Between Object, Image, and Visual Spaces

Light may arrive from all directions at any point in an illuminated environment so that global information about the visual organisation of the surroundings is potentially available to an eye wherever its anterior nodal point is situated. No eye can accept light from much more than a hemispherical field, and two are only just capable of providing complete coverage of the surroundings if they are appropriately positioned relative to one another. Even then, only that portion of the total optic field which is served by retina can be significant in the determination of the behavioral capacity of a species.

The topographic organisation of the visual environment is retained in its projective transformation into the retinal image and remains embodied in several subsequent central stages of neural processing as well as providing a substrate for the organisation of the motor system in terms of external space (e.g., APTER, 1946). Oculocentric distance along visual lines of direction in object space (HERING, 1879) transforms into a continuum of conjugate image space shells which may be selectively brought to the effective receptor plane by an accommodatory mechanism. Relative and absolute depth information is potentially available from the slight differences between the retinal images of the common field of the two eyes. In some species, at least, this binocular parallax is detected by the neural mechanism of receptive field disparity (BISHOP, 1973) which appears to underlie the faculty of stereopsis. The intrinsic limitations on the maximum size of the uniocular retinal field mean that there is a tendency for an inverse relationship to exist between the extent of the binocular and lateral visual fields in a given species. The balance between the extent of the two fields, and thus the proportion of the global array to which the species has parallel access, must be subject to considerable selective pressure and does not correlate well with phylogenetic status; what ecologic and behavioral factors actually determine the width of the binocular field remains to be established.

GIBSON (1950) emphasised that visual information about environmental organisation is primarily contained in the intensity variations of light arriving from different directions (but see BOYNTON, 1975). Thus, at a *point of observation*, he distinguished the *ambient optic array* from ambient light as:

> A nest of solid angles, not rays, each solid angle corresponding to one of the large faces or small facets of the environment. The solid angles are separated by contours or contrasts.

The flow of structural information between object and image may be treated directly (GABOR, 1961; WINTHROP, 1971) or, more conventionally, in terms of the quantal nature of light which sets the ultimate limit on the information capacity of the ambient optic array. Of course, the eye can never attain this capacity; the mamalian eye is effectively insensitive to polarisation and thus the accessible

potential information of the ambient array is reduced by 50%; again, losses in the ocular media may amount to some 50% of the light incident on the cornea and of this perhaps only 20% is absorbed by photopigment (HECHT et al., 1942). Thus, under the conditions of a typical calculation (HISDAL, 1967), the *foveally* detectable information in a photopic photon beam amounted to only $1/10^5$ of that potentially available. Although the information content of the ambient optic array is substantially lost in the formation of the image at high levels of illumination, it is found that noise arising from the statistical fluctuation in photon arrival at low intensities may so limit the spatial information content of the array that the optical apparatus of the eye is equal to its efficient transfer to the image plane and the neural equipment to its detection; under these conditions the match between the information capacity of the ambient array and of the eye is much better. Within the eye, however, at even low photopic levels the quantal nature of light must be taken into account during high resolution tasks (PIRENNE, 1962; COHN, 1976).

Scatter, diffraction and aberrations of the optical system are more significant factors than quantum efficiency in setting a limit on the transfer of information from the ambient optic array to the image space; the efficacy of this process is summarised by its three dimensional modulation transfer function (FRIEDEN, 1967). The neural apparatus only samples that shell of the image space, the effective image shell, which is intersected by the photoreceptor apertures and whose information capacity is described by a surface modulation transfer function. The potential information of the effective image shell is even further reduced by the effects of retinal sampling grain and noise introduced during retinal transduction and transmission. For an idealised retina, SNYDER et al. (1977) have considered the influence of the above factors on information capacity defined as a function of the number of discriminable intensity levels and resolvable points, ‚the number of discriminable pictures.' For a specific sampling grain this measure of information capacity may be shown to be optimal at a given level of illumination.

A 2.4 mm diameter human pupil strikes an optimal balance between the deleterious effects of diffraction and aberration on the retinal image quality and this is expressed in the corresponding maximal image spatial cut-off frequency, f, of some 60 cy/°. In accordance with SHANNON'S (1949) sampling theorem for optimal systems the foveal cone separation is found to be matched to this cut-off frequency at a value of $(1/2f)°$. One-to-one connectivity between foveal photoreceptors and ganglion cells (MISSOTTEN, 1974) ensures that this potential for optimal resolution is relayed to the CNS with the result that maximum behavioral acuity almost attains the value of optimal resolution in the retinal image.

Convergence of connectivity from photoreceptors to ganglion cells ensures that, outside the foveal centre, the latter set the upper limit on *neural* resolution but whether neural or optical factors predominate in limiting overall peripheral acuity remains an equivocal question. No satisfactory human peripheral MTF measurements have been made to establish optical quality and very little peripheral acuity data is available from which optical influences have been excluded. In conjunction with the unavailability of satisfactory ganglion cell distributions for man it is not surprising that the question of whether neural sampling in peripheral retina is optimally matched to the image remains undecided at present. WEALE (1976) has suggested that the total peripheral photoreceptor density of man is well matched to the number of degrees of freedom in the local retinal image but his computations are based on geometric considerations and do not incorporate the influence of oblique aberrations on the local MTF.

The possibility of locally matching neural and optical resolution is a simple example of many possible strategies which the CNS may employ to avoid redundancy and achieve an optimal system (ATTNEAVE, 1954; BARLOW, 1961). A comparative survey indicates that the optic quality and retinal provision for different regions of the optic array are rarely uniform and vary considerably between species. The great anisotropy of ganglion cell distribution in some species indicates that the overall neural sampling distribution of the retina is definitely not matched to the more symmetrical variation of image quality. Such optic and retinal heterogeneity could reflect adaptive minimisation of redundancy by matching of the sampling apparatus to a required subset of the information distributed in those invariant features of the retinal image, the overt image of the visual horizon or the less obvious flow patterns which occur during locomotion, which arise out of its projective relationship with the environment. Alternatively, like the balance between the overall extents of the binocular and total fields of view or the local specialisation of a retinal region for photopic colour vision, it may arise as an adaptive solution to the conflicting requirements of the species life style and not from anisotropy of the image, optic array, or environment. In spite of such differentiation of the optics and retina, it remains

possible for the isotropic potential of the optic array to be exploited in full by serial sampling which involves eye, head and body movements whose extent and frequency may, therefore, be expected to correlate with the various specialisations in retinal topography.

It is generally established for vertebrate species that the visual apparatus does not simply relay the variations in light intensity across the retinal image. Early mammalian single unit recordings, first by KUFFLER (1953) in the retina and HUBEL and WIESEL (1959) in the visual cortex, revealed that many receptive fields at these levels are organised in the cat for the detection of contrast and contour, respectively. The visual system is thus appropriately equipped in this animal, and man, with the neural apparatus for the extraction of the optic array from ambient light in accordance with GIBSON'S (1950) psychophysical theories. It appears possible, but not certain however, that the manner in which visual information is processed both peripherally and centrally may be different in other mammals depending upon whether they are organised for frontal or lateral vision.

At the distances encountered in terrestial, but not astronomical, observation, the abstraction of the everyday physical world exemplified in the infinite rectangular coordinate system of Euclidean space appears to be very accurate. The projective transformation of the external world into a spherical image space results in general distortion of relative object separations, dimensional changes when objects recede or approach and other non-Euclidean phenomena. The subjective *visual space* which is centrally derived from the retinal image is further dependent upon the nature of the transformations effected by the retinal and subsequent neural processes and might not be expected to be Euclidean. Although many reports have been made of anisotropies in subjective visual space (HELMHOLTZ, 1924; LE GRAND, 1967; PIRENNE, 1970), and it has been suggested that the metric of binocular space is hyperbolic (LUNEBERG, 1947), the majority of such anomalous perceptions are difficult to demonstrate and not universally accepted as occurring. The mature human observer appears capable only of a projective, rather than a Euclidean, interpretation when faced with dynamic figural transformations, and thus assumes a rigid Euclidean organisation of the stimuli (GUNNAR JOHANSSEN, 1975). Higher-level processing effectively inverts the projective transformation in man, thus giving rise to phenomena like size constancy (LEGRAND, 1967) and ensures a subjective visual space which corresponds quite closely in its properties to a Euclidean abstraction rather than to a retinal image space.

The gross correspondence between the properties of human visual space, whether subjectively or behaviorally established, and those of Euclidean space indicate that the various stages of visual processing are effectively "transparent." If there is advantage for man in this arrangement, it seems probable that it will occur in other species. In spite of the obvious differences between the optic arrays of various environments, it remains that the underlying spatial, metric, and optical principles are common to all species and, in spite of gross differences in neural substrate, their subjective visual spaces might therefore be expected to be similar to that of man in qualitative, if not quantitative, properties. The visual space of other species is, of course, only accessible through behavioral techniques and has not yet been subject to serious investigation. An underlying uniformity of perception across a wide range of classes of animal, however, is implicit in the universal effectiveness of the few principles of camouflage employed throughout the animal kingdom (COTT, 1966). If the MÜLLER-LYER illusion does indeed have its origin in perspective effects (GREGORY, 1963; GREGORY and HARRIS, 1975) then perhaps it should not be surprising that both fly and man are subject to it (GEIGER and POGGIO, 1975).

B. The Field of View of the Animal

I. The Uniocular Optic and Retinal Fields

The uniocular field of vision behaviorally demonstrable in an animal has in the past been treated as equivalent to the field of view of the eye's dioptric apparatus subject to its restriction by the optic adnexa. The long-standing assumption that the extent of the retina is not a factor which limits the extent of the behavioural fields of view was first made explicit by VAKKUR and BISHOP (1963) in

their cat schematic eye, but has since been demonstrated to be invalid in that species (HUGHES, 1976a). It is consequently necessary to define two distinct *uniocular* fields: (1) the *optic field of an eye*—the solid angle subtended at its anterior nodal point by that region of visual space from which light may be refracted through the lens; and (2) the *retinal field of an eye*—that portion of its optical field which is encompassed by the external projections of its retinal margins.

The absolute uniocular fields are measured on the freshly enucleated eye or in situ if the field is free of obstruction by the nose and optic adnexa. The relative, or obscured, field includes the influence of the adnexa and must be measured in situ.

Most published measurements of the extent of the uniocular field have been obtained with the technique of transcleral illumination. TSCHERMAK-SEYSENEGG (1902), ROCHON-DUVIGNEAUD (1922), and other workers assessed the horizontal angular range over which light from a small source was refracted into the eye by viewing its image transclerally. The technique was extended by THIEULIN (1927) and PISA (1939) to other planes. Although commonly accepted as satisfactory (WALLS, 1942; DUKE-ELDER, 1958), this method establishes the extent of neither the optical nor the retinal fields; in the cat it indicates (VAKKUR and BISHOP, 1963) a field of greater extent than the uniocular retinal field yet smaller than the optical field. The perimetric determination of the ophthalmoscopically observed limits of the retinal uniocular field reveals that it serves only 143° of the 181° cat uniocular optic field and some 179° of 200° in man (unpublished observations). By contrast, the 192° rabbit (PISA, 1939; HUGHES, 1971, 1972) and 205° rat (LASHLEY, 1932; HUGHES, 1977c) uniocular optic fields are entirely served by the retina. These and other unpublished observations substantiate the belief that the uniocular optic field is of relatively constant size in most species but WALLS' (1942) view that

> the cone of space subtended by the retina is surprisingly uniform throughout the vertebrates. It is rarely much greater or less than 170°

appears to be ill founded; the uniocular retinal fields of the cat and rat alone range from 143° to 205°, respectively. Obviously the uniocular retinal field must replace the optical field in consideration of the behavioural range of vision in a given species; calculation from the dioptric apparatus (VAKKUR and BISHOP, 1963) is not adequate.

II. The Cyclopean Fields

1. Nomenclature

The horizontal separation of the two eyes, advantageous because the resulting disparate retinal images enable binocular depth perception, introduces a difficulty into the specification of the fields of view *of the animal*. For this purpose a single reference point is required relative to which the angular projections of the ophthalmoscopically observed delimiting landmarks of the fundus may be subtended. The cyclopean projection centre situated half-way between the anterior nodal points of the two eyes (HELMHOLTZ, 1924) has been adopted for this purpose. In the limit, at measuring distances so great that the interocular separation is relatively negligible, the cyclopean projection point and the anterior nodal

points are effectively coincident. We thus define two *cyclopean* static visual fields for the animal with its eyes in the primary position, i.e., centred in the head with their visual axes parallel:

The *cyclopean optic field of an animal* is the solid angle subtended at the cyclopean projection centre by those regions of space from which light may be refracted through the lens of either eye.

The *cyclopean retinal field of an animal* is that portion of its cyclopean optical field which is encompassed by the external projection of the retinal margins of *either* eye.

So defined, the angular limits of the optical and retinal cyclopean fields are the same as for the corresponding uniocular fields when referred to the visual axes. This would not be true for closer measurement distances. The absolute or relative fields must be established from the measurements of the appropriate uniocular field.

The *nasal limits* of either the retinal or optical uniocular fields determine the corresponding binocular fields.

The *binocular field of an animal* is that common portion of either cyclopean retinal or optic fields from which light may be simultaneously refracted through the lenses of both eyes. Both relative and absolute fields may again be derived.

2. Measurement and Construction

The extents of the binocular and panoramic fields of view were at first indirectly assessed. MÜLLER (1826) employed the angle between the orbital margins to make estimates of the binocular field, but the relationship varies extensively between species. A rough idea of the degree of laterality of the eyes in different forms may be gained from the divergence of the corneal axes (GROSSMAN and MAYERHAUSEN, 1877) or the optic axes (Fig. 1) (JOHNSON, 1901). The subsequent, more direct, estimates of fields based upon transcleral illumination (ROCHON-DUVIGNEAUD, 1922) suffer from similar defects to those of the uniocular fields and require, with the possible exception of estimates of the relative binocular fields, replacement by measurements based upon direct observation of the fundal landmarks.

The elimination of eye movements and assurance of the primary eye position are difficult to achieve in the conscious animal so that the relative cyclopean fields are not determined directly. The rabbit is an exception to this generalisation because of the "freeze" posture elicited by a loud noise. In this condition the eyes return to the primary position for a sufficient length of time to permit the cyclopean fields to be directly measured (HUGHES, 1971).

The cyclopean fields of species whose fixation area is ophthalmoscopically well defined, such as cat, monkey, and man, are instead constructed from the appropriate relative or absolute uniocular fields by superposition of the visual axes. In such animals the ability to define the visual pole and projection of the visual axis enables the anatomic position of rest of the eyes in the paralysed or dead preparation to be compared with the primary position. In man (DUKE-ELDER, 1932) and cat (BISHOP et al., 1962) the difference is small. If this is true of

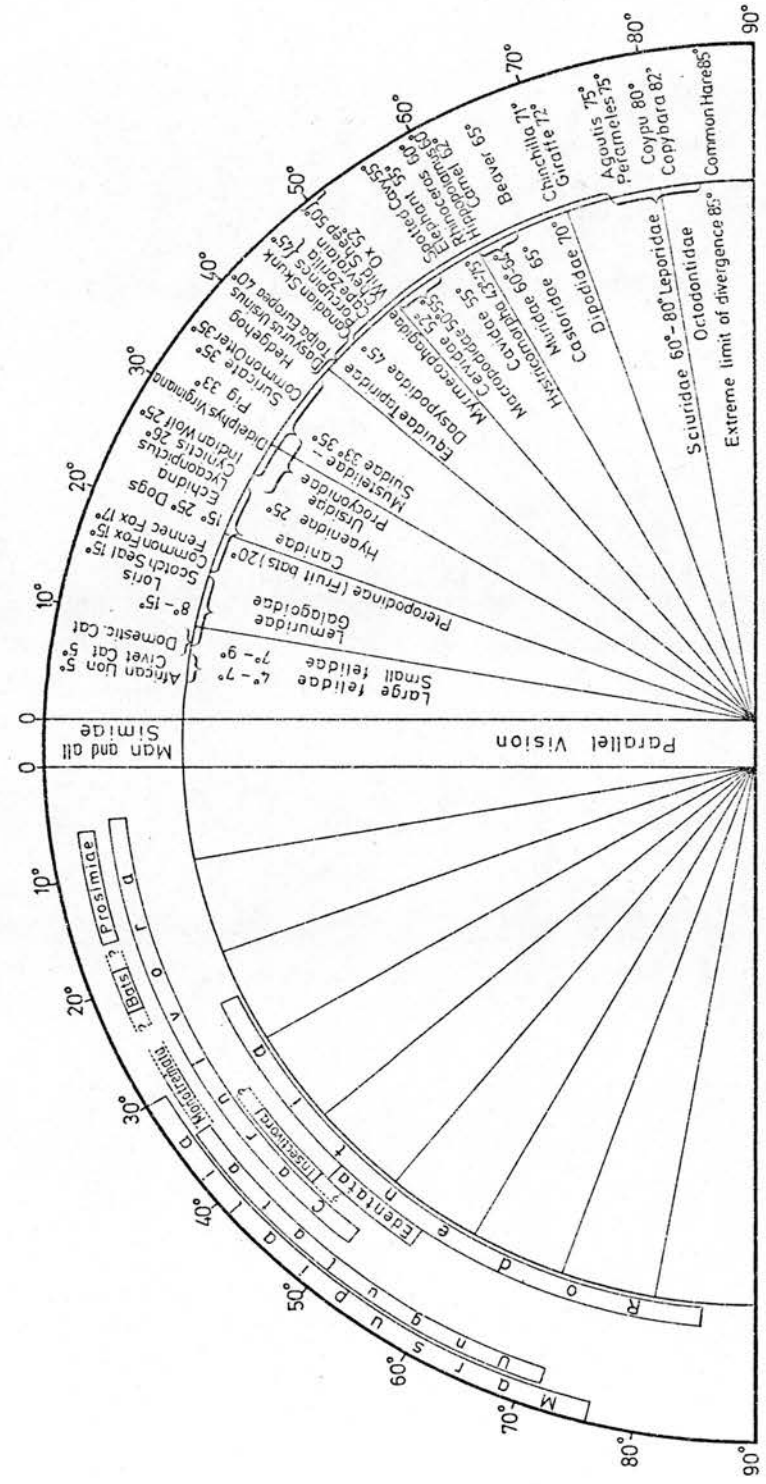


Fig. 1. Divergence of the optic axes in the mammalia; a crude index of binocular field width (after JOHNSON, 1901)

other forms, the results of PISA (1939) and other workers may acceptably define the binocular fields of the conscious animal.

In rabbit, rat, and other species the fixation area is not ophthalmoscopically visible, and examination of the retinal ganglion cell distribution does not enable a visual pole to be specified accurately with respect to the projection of some other visible landmark. The error entailed in acceptance of the fields defined for the anatomic position of rest as a substitute for those in the primary position cannot be assessed nor the cyclopean be constructed from the uniocular fields when the projection of the visual axes is unknown. Indeed, according to DUKE-ELDER (1958),

> unless there is an area centralis of acute vision ... the whole concept of fixation along a visual axis is meaningless; only in those animals provided with an area of acute vision is such a concept possible ...

In spite of the absence of an obvious visual pole both rat (LASHLEY, 1938) and rabbit (VAN HOF and LARGERS VAN HASELEN, 1973) behave as if they possess a fixation axis projecting dead ahead which suggests, contrary to DUKE-ELDER'S generalisation, that some part of the retina may be functionally differentiated.

In man (VAN BUREN, 1963), monkey (STONE et al., 1973), and cat (STONE, 1966) the gross, histologically defined decussation line passes through the fixation area. Although the decussation line of neither rat nor rabbit has been defined anatomically, its cortical representation as the boundary between the electrophysiologically mapped areas VI and VII has been specified in terms of its projection into the visual field relative to that of the optic nerve head [rat (ADAMS and FORRESTER, 1968; MONTERO et al., 1968; MONTERO et al., 1973), and rabbit (THOMPSON et al., 1950; HUGHES, 1971)]. In both species the plane of projection of the decussation line contains the behavioural fixation axis; by analogy with cat and monkey, it is presumed that the functional visual axis also lies in this plane so that the cyclopean may be constructed from the uniocular fields.

3. Extent of the Cyclopean Panoramic Field

The absolute cyclopean fields of the rabbit (HUGHES, 1971), rat (HUGHES, 1977c), and cat (HUGHES, 1976a) are presented in Fig. 2 as constructed according to the previously outlined principles from ophthalmoscopically defined uniocular fields. The remarkable differences between the visual fields of frontal and lateral eyed species are well illustrated.

The whole field of the rabbit encompasses nearly an entire sphere, but contrary to earlier reports (DUKE-ELDER, 1958), there is no sign of binocular overlap to the rear of the head in the horizontal plane (HUGHES, 1971), although such a field exists at greater elevations (PISA, 1939; HUGHES, 1971). Again, the alleged 287° horizontal field of the cat (THIEULIN, 1927; DUKE-ELDER, 1958) has not been confirmed (HUGHES, 1976a); the cyclopean optical field of the cat extends for only 210° and the retinal field for 187°. The blind field to the rear of the cat in the horizontal plane is thus 173° compared with 1° or 2° in the rabbit. The extent of these estimated cyclopean fields is substantially confirmed for the cat by the behavioral measurements of SHERMAN (1973).

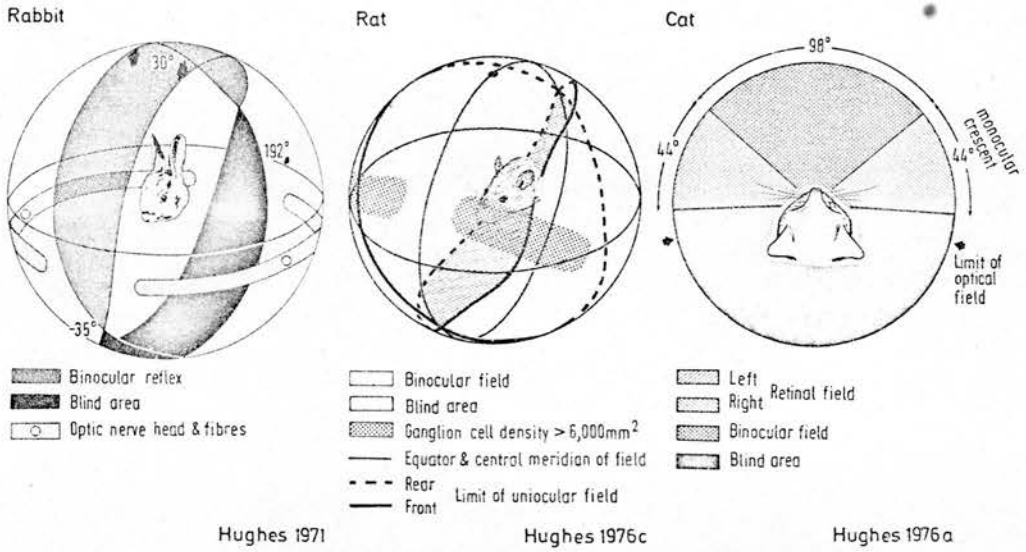


Fig. 2. Ophthalmoscopically defined absolute ocular fields of the rabbit, rat, and cat. The equatorial cyclopean fields of rabbit and rat are almost equally extensive, but, in spite of this, rat binocular field is almost three times wider than that of the rabbit; it is obvious that the extent of binocular and cyclopean fields need not vary in strict inverse ratio. Cat binocular field is only slightly wider than that of the rat, but its cyclopean field is much more restricted in extent; cyclopean field width is thus not a simple passive consequence of the binocular field width, and its limited extent in the cat is an adaptive feature of the frontal syndrome (HUGHES, 1972, 1976a, 1977c)

The extensive horizontal panoramic fields of the rabbit, 360°, and rat, 320°, are attained by retinal exploitation of the entire uniocular optic field. The less extensive panoramic field of the cat is compatible with a 38° difference between the retinal and uniocular optic fields (HUGHES, 1976a). The discrepancy between optic and retinal uniocular fields of view may thus generally be greater for frontal than for lateral eyed species.

4. Extent of the Binocular Field

The rat may be described as possessing lateral eyes, its 320° panoramic field exceeds that of the cat by some 135° and approximates the 360° of the rabbit, yet it possesses an 80° binocular field (HUGHES, 1977c) which approximates the 99° of the cat (HUGHES, 1976a) and considerably exceeds the 24° of the rabbit (PISA, 1939; HUGHES, 1971). The extensive binocular and panoramic fields of the rat arise from the retinal exploitation of its large uniocular optic field.

It is very noticeable that the spherical panoramic fields of view of the rat and rabbit are accompanied by extensive upper binocular fields. It has not been established whether these regions are binocularly represented at the cortical level or whether the animals attain stereoscopic vision in them. In man, monkey, and cat, the upper field of view is very limited.

The striking contrast between the elevated optic axis of ground dwelling species such as the rabbit and rat and its depression in a taller species with little to

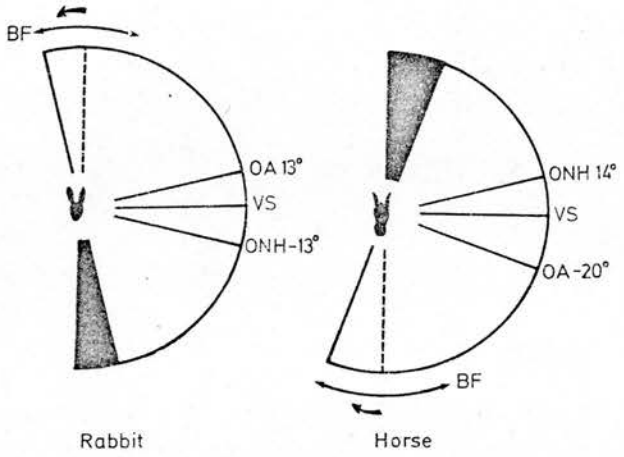


Fig. 3. Coronal sections through absolute visual fields of rabbit and horse. The rabbit, which is vulnerable to aerial predators, shows upper-field binocular overlap, *BF*, but the larger, cursorial horse has binocular overlap in region of inferior field occupied by forefeet. Lateral projection of the visual streak, *VS*, optic axis, *OA*, and optic nerve head, *ONH*, are also indicated (HUGHES, 1971, and unpublished observations)

fear from elevated predators is revealed by comparison of coronal sections of the uniocular field of rabbit and horse. The horse possesses an effective binocular field below its head (PISA, 1939), the inverse of the arrangement in the rabbit (Fig. 3).

The recent quantitative revisions of the visual fields in species so familiar as cat and rabbit suggest that the literature dealing with more exotic forms requires confirmation before its detailed consideration. The qualitative description of the fields in other species which is provided by WALLS (1942), ROCHON-DUVIGNEAUD (1943) and DUKE-ELDER (1958) is probably sufficiently accurate for general purposes.

III. The Functional Basis of Species Differences in the Extent of Panoramic and Binocular Fields

1. Panoramic Field

XENOPHON (1905) describes the hare as lacking

> keen sight, for many reasons: for it has its eyes prominent and the lids small, affording no protection for the eye balls; and their sight is on this account dim and dispersed.

According to the Greek centrifugal theory of vision, the wide field of sight is disadvantageous, but the modern centripetal theory indicates that for such hunted species

> there can be no doubt that the divergence of the optic axes combined with a large cornea, is a great source of protection to the animals by the increased range of vision it gives them

(JOHNSON, 1901). The hare and rabbit, both with the habit of "freezing", can spot enemies coming in any direction without a revealing head or eye movement. In spite of this advantage, the cyclopean retinal, or panoramic field, is effectively absent to the rear of the head in frontal eyed species such as primates and carnivores. Why is this so?

According to WALLS (1942):

> the visual field of the single eye is roughly constant at 170° or so (thus), we may consider the angular width of the binocular field to be quite directly related to the angle between the two optic axes, which in itself will depend upon the position of the eyes in the head.

The binocular and panoramic fields would thus vary inversely in extent. Given WALLS's (1942) belief in a universal

> urge to binocularity

then a trend towards the disappearance of the rear panoramic field would appear to be inevitable.

The previous demonstration that the uniocular retinal field may vary over a considerable range between species means, however, that the magnitudes of the binocular and panoramic fields may, in general, attain some degree of independence of each other. It certainly remains true that the limitations on the extent of the uniocular optic field ensure that only a small binocular field is possible in those lateral-eyed species for which, because of defencelessness or lack of cover in their environment (WALLS, 1942), an almost complete panoramic field of view is vital. But the suggestion that

> binocular animals have made a sacrifice: they have abandoned the enormous biological advantage of panoramic vision in order to have their eyes pointing forward

(BLAKEMORE et al., 1972) it not the primary explanation. The rat attains a large binocular field, only 20% smaller than that of the cat, but its large uniocular fields generate a panoramic field 72% more extensive than in the cat (HUGHES, 1977c) and only slightly smaller than that of the rabbit. The absence of a panoramic field to the rear of the head in frontal species is not universally restricted by the limited extent of the uniocular field alone. Some 38° of the cat, and 30° of the human uniocular fields remain unserved by retina and would be thought to be potentially available to extend the field to the rear of the head without reduction of the binocular field (HUGHES, 1976a).

The loss of the rear panoramic field in frontal species possibly arises out of a need for parallel or only slightly divergent *optic axes*, the adaptive significance of which is discussed later, when the extent of the temporal uniocular optic field cannot be increased. That loss of the rear panoramic field is acceptable as secondary to some other requirement in these species is perhaps more indicative of a false attribution of importance to it in their life styles than of a "sacrifice" on their part.

> The predaceous animal can afford not to have such "eyes in the back of his head," because his offensive weapons, teeth and claws, give him immunity from stealthy attack

(WALLS, 1942). This observation is in keeping with the presence of more lateral eyes in those small predators, such as weasels, which are themselves preyed upon but does not account for the extensive blind regions to the rear of the head in the poorly armed and nonpredaceous primates. However, only

> a few specialised arboreal mammal-eating predators have been developed, including snakes, monkey-eating eagles, and several carnivores. But on the whole arboreal animals are less subject to predation than terrestial forms. Many are relatively unarmed, and depend upon inconspicuousness (sloths), unpalatibility (koalas) or rapid escape (squirrels and monkeys)

(HAINES, 1958).

Consideration of the static cyclopean fields is a very limited approach. The disappearance of the rear panoramic field in frontal species is much less significant when the mobility of the eyes and head are taken into account. The *static* cyclopean retinal field of man extends for only 208° (HARTRIDGE, 1919) compared with the horizontal limits for the *dynamic* field of 288°. Even the 72° dynamic blind area to the rear of the head is totally eliminated if the head is permitted to rotate.

2. Role of the Binocular Field

Stereopsis. Among mammals only the larger whales are said to lack a binocular field, but what advantage is obtained by its possession? The human binocular absolute luminance threshold for 50% seeing is 0.1 $\log_{10}$ units lower than the uniocular threshold (PIRENNE, 1962). Visual acuity (BÁRÁNY, 1946) and the threshold contrast for sinusoidal gratings (CAMPBELL and GREEN, 1965) are improved to a similar extent in binocular relative to uniocular viewing. Such threshold benefits have been suggested to be the reason for the development of a binocular field in abyssal-fishes and owls (WALLS, 1942), but among the mammals, at least, the frontal binocular field is generally regarded as the substrate for stereoscopic depth perception (BISHOP, 1973), in which the relative separation of objects in depth is determined from the disparity between the retinal images of the common field of the two eyes. JOHNSON (1901) rejected BERLIN's (1893) assumption that this ability should be attributed to all species evincing depth perception, because monocular individuals perform equivalently in many tests; this conclusion has been supported by many later experiments (WALK, 1965). The isolation of binocular disparity (see BISHOP, 1973) from monocular cues for relative depth has, however, become relatively straightforward since the advent of the anaglyphic random dot stereogram (JULESZ, 1971) which has already been employed to demonstrate stereopsis in the monkey (BOUGH, 1970). The cat alone among the remaining mammals has been tested for stereopsis, by another method, and was concluded to possess it (FOX and BLAKE, 1971); more recently, the range of fusion and quantitative stereopsis have been established in the same animal (PACKWOOD and GORDON, 1975).

The low ganglion-cell density at the fixation area and small interocular distance of many small mammals has been regarded as an inadequate basis for useful stereopsis. It is true that the theoretical maximum stereoacuity of these species appears poor when compared with that of man, if expressed as an angle, but its

value is of greater significance in terms of a linear displacement *over the range of interest to the animal*. High angular thresholds may be quite adequate for small animals which are concerned with nearby objects.

The neural mechanism of stereopsis in mammals (BISHOP, 1973) is believed to depend upon *partial* decussation at the chiasma and subsequent convergence of the projections of the left and right hemiretinas to cells selectively sensitive to image disparity. Such cells have been recorded in monkey (HUBEL and WIESEL, 1970), cat (BARLOW et al., 1967; NIKARA et al., 1968) and goat (CLARKE and WHITTERIDGE, 1976). The established presence of the whole or part of this apparatus in a mammalian species would be presumptive evidence for stereopsis.

Stereopsis in Lateral-Eyed Species. The phrase "binocular vision" is rarely defined, yet clearly has not the same implications to all authors; an unfortunate situation, because its use is often accompanied by judgments of its relative quality in different species. Common usage tends to equate frontality with binocular vision

> among the mammals only the carnivores, lower primates and man have developed binocular vision to any extent ...

(BISHOP, 1973). For HARTRIDGE (1952) the binocular fields of

> animals in which the two eye axes are parallel have the greatest overlap, and therefore possess the most perfect binocular vision

with "a single mental impression" over the widest field. But these usages fail to separate consideration of the binocular field width from that of stereoscopic vision quality. The inevitable outcome is that it is still common to find the corollary of the above judgements, that binocular vision is poorest in lateral eyed species, is used to imply that they also lack stereopsis (ELLIOT SMITH, 1930; CARTMILL, 1974)

> Laterally placed eyes, of course, preclude stereoscopic vision

(VINCENT, 1912). If binocular vision is primarily concerned with stereoscopic depth judgement, as previously argued, then comparison of its quality between species would best be made in terms of their differences in eye separation, visual acuity or behaviorally determined stereoacuity. Discussion of the variations in binocular field width is taken up again subsequently.

The continued implicit belief that in lateral-eyed species

> this great range of lateral vision makes, of necessity, vision in the direct line ahead correspondingly bad

(HARRIS, 1904) may provide supplementary reasons for the neglect of the limited binocular field of many such animals. It has, however, not received experimental justification and usually appears ill-founded in either confusion of the optic and visual axes or the well-entrenched, but not necessarily valid, belief that peripheral optics must be so poor as to inevitably preclude adequate forward vision.

The 360° panoramic field of the rabbit (PISA, 1939; HUGHES, 1971), 320° of the goat (HUGHES and WHITTERIDGE, 1973), and 300° of the grey squirrel (HALL et al., 1971; LANE et al., 1971) qualify these animals as lateral eyed. Many workers would thus not describe them as binocular species in spite of the potential for

stereopsis in their respective 24°, 60°, and 60° binocular fields. In the goat the temporal fixation area some 50° divergent from the optic axis is yet of potential neural resolution better than that of the cat (HUGHES and WHITTERIDGE, 1973), thus suggesting that its peripheral optics are good. The adequacy of the peripheral optics of rabbit and squirrel is implied in their use of the binocular field as their behaviorally favoured fixation area (VAN HOF et al., 1973; POLYAK, 1957). Presumptive evidence for the presence of stereopsis is also available. The electrophysiologically mapped cortical representation of the binocular field receives a bilateral input in rabbit (THOMPSON et al., 1950; HUGHES, 1971), goat (CLARKE and WHITTERIDGE, 1976), and squirrel (HALL et al., 1971; LANE et al., 1971). This binocular area contains disparity-sensitive binocular neurones in both rabbit (VAN SLUYTERS and STEWART, 1974a) and goat (CLARKE and WHITTERIDGE, 1976), but such cells need not unequivocally establish a substrate for stereopsis. JOSHUA and BISHOP (1970) suggest that the equal vertical and horizontal disparity sensitivity of cat visual area I neurones rather implicates them in the mechanism of binocular fusion. However, in the sheep at least, horizontal disparity sensitivity appears to predominate in the binocular neurones of visual area II (CLARKE et al., 1976), and they are described as organised into "depth" columns similar to those reported for the cat by BLAKEMORE (1970). The good depth judgement of sheep (WALK and GIBSON, 1961), the well-known agility of goats.

> In North Africa domestic goats are becoming pests of fully grown fruit trees, for they have learned to climb on high branches and browse off the foliage.

(HAINES, 1958)—and of squirrels (CARTMILL, 1974; POLYAK, 1957), also strongly imply the possession of stereopsis in these species.

A recent extensive study of single units in the rabbit binocular area (VAN SLUYTERS and STEWART, 1974a, 1974b) places great emphasis on differences between their organisation and that of the corresponding units of the frontal-eyed cat. Disparities for many units were so large as to appear nonfunctional; binocular units often had as inputs two different classes of receptive field, and developmental plasticity was markedly lacking (VAN SLUYTERS and STEWART, 1974b; CHOW and SPEAR, 1974). But while awaiting confirmation of these features, it is worth emphasising the *correspondences* between rabbit and cat binocular cortex organisation; some 70% of the rabbit units *were* binocular; 50% *did* have similar inputs from each eye and *some* disparities were in a range that could be functionally useful. These components of the cortical apparatus could alone suffice to provide a substrate for stereopsis in spite of the puzzling anomalies.

At present there is a great deal of evidence to support the view that many features of organisation in the central provision for the binocular field are common to forms with frontal or lateral eyes, and it would be wise not to dismiss the possibility of stereopsis in any species of mammal which possesses a binocular field.

Stereopsis Among Nonmammalian Vertebrates. Since WALLS (1942) said of stereopsis.

> There is no more vexed question in all of comparative ophthalmology than the one whether this binocular factor in depth perception exists for vertebrates below the mammals,

there has been little progress towards a solution. A binocular field is present in nearly all vertebrates, but in the opinion of many workers (HARRIS, 1904; COLLINS, 1921), although not all (WALLS, 1942), the alleged absence of a partial retinal decussation precludes the possibility of stereopsis in the nonmammalian classes. Thus INGLE (1970) regarded the frog as lacking stereopsis and attributed its depth perception to motion parallax or information from an accommodatory center (INGLE, 1968). However, from the functional point of view it is not important whether decussation occurs at the chiasm or at some subsequent stage in the visual pathway. The tectal representation of the binocular field in the submammalian species has been most thoroughly examined for *Rana* and *Xenopus* and found to obtain an input from both eyes (GAZE and JACOBSEN, 1962; KEATING and GAZE, 1970; GAZE et al., 1970); the ipsilateral retinotectal projection arises from the contralateral tectum and passes to the ipsilateral side via the postoptic commissures (KEATING and GAZE, 1970). Cells in the binocular area respond to inputs from either eye (FITE, 1969; SKARF, 1971) between which predominantly horizontal disparities have been demonstrated in unparalyzed preparations (RAYBOURN, 1975), thus providing a mechanism for the stereopsis previously suggested only by the presence of an ipsilateral tectal representation. A similar ipsilateral projection has been reported for the axolotl (BRÄNDLE and STIRLING, 1975). A recent examination of the influence of lenses and prisms on snapping behaviour in toads (COLLET, 1977) indicates that, under monocular conditions, the distance of prey is judged by means of accommodatory cues in agreement with INGLE's hypothesis (1970; 1971; 1972; 1973) but that disparity cues were employed during binocular judgements.

The presence of superposed ipsi- and contralateral projections in the tectal representation of the binocular field has not been established for other nonmammalian vertebrates, such as fish (JACOBSEN and GAZE, 1964; SCHWASSMAN and KRUGER, 1965; SCHWASSMAN, 1968), alligator (HERIC and KRUGER, 1965), or pigeon (HAMDI and WHITTERIDGE, 1954). A detailed search for an ipsilateral representation in the tectum of foveate marine teleosts was not successful and revealed binocular activation only in the nucleus praetectalis (SCHWASSMANN, 1968). Four binocular units were recorded in the pigeon cerebellum (CLARKE, 1974). However, other regions of the brain in these species remain unexplored. A very recent report (PETTIGREW and KONISHI, 1976) described the visual "Wulst" of the owl as containing many binocular neurones, in spite of an allegedly monocular thalamus, the characteristics of which are similar to those of cat and monkey visual cortex. Tests for stereopsis were described as "promising." It thus appears probable that investigation of the telencephalic regions of other submammalians will reveal binocular organisation and that, in common with WALLS (1942), we might feel justified in regarding the presence of the binocular field in these classes as presumptive evidence of stereopsis. Whether or not we would *be* justified remains to be seen, at least for species with independent eye movements. HARKNESS (1977) has made a convincing demonstration, although not employing pure disparity cues, that chameleons base their judgement of prey distance on accommodatory cues under both monocular and binocular conditions. However, the animal remains untested for ability to sense pure disparity cues.

It is somewhat ironic, now the reality of a supraoptic, chiasm has been demonstrated in the owl, that early suggestions (see PRINCE, 1956) of a decussation in

reptiles and snakes should be gaining support from work on another nonmammalian species. A genuine, primary, ipsilateral projection from the retina is now established as present in the frog (LAZAR and SZEKELY, 1969; CURRIE and COWAN, 1974), but it does not supply the tectum. Its physiologic significance remains to be established.

3. Teleology of Binocular Vision

The Relationship Between Binocular Field Width, Phylogeny, and Life Style. Binocular vision is almost universal amongst the vertebrate species in the majority of whom it presumably provides a basis for stereopsis. Any explanation of the variability of binocular field *width* between species would therefore be expected to be generally applicable amongst the vertebrate classes.

The absolute horizontal extent of the binocular field in both fishes and reptiles is said to rarely exceed 40° (KAHMANN, 1930, 1935), while the upper limit for birds, with the exception of some raptorial species, is about 50° (WALLS, 1942). Although these measurements still require confirmation, their contrast with the mammalian range of 25°–100° for the subprimates and up to 130° for the primates is obvious to direct inspection. Among the nonmammalian vertebrate classes, the anurans contain the only known species which attain binocular fields as wide as those to be found in the higher mammals; in *Rana* and *Xenopus* the binocular field is from 80° to 100° wide (GAZE and JACOBSEN, 1962; GAZE et al., 1970). Similar observations led JOHNSON (1901) to the conclusion that the width of the binocular field, and in his opinion the inversely related extent of the panoramic field is determined by the phylogenetic status of the species,

> the higher the order, the nearer the axes approach parallel vision, although the range is considerable ...

The possession of an extensive panoramic field was even regarded by some as a "primitive" feature (PARSONS, 1927).

Although adopted by a few later workers (PARSONS, 1927; POLYAK, 1957), the hypothesised phylogenetic correlation was contemporarily challenged by HARRIS (1904),

> the presence of binocular vision in animals seems to depend upon their feeding habits rather than upon their social position, if I may use the term, in the animal scale ... lateral placed eyes being found for the most part in the herbivores and rodents, that is to say, in animals whose food does not run away from them, whilst the most perfect binocular vision is found in the carnivora ... and in the primates.

HARRIS (1904) realised the difficulty of applying his generalization to the submammalian classes when couched in terms of absolute binocular field widths and was suitably cautious. Subsequent results have shown, however, that within one class it is often true that predators possess wider binocular fields than prey. The binocular fields of predatory fish, such as trout or pike, 30°–40° (KAHMANN, 1935), may be of twice the width of those in herbivorous or bottom-feeding fish, 10°–20° (WALLS, 1942). Among reptiles the same trend is to be found; the herbivorous *Testudo* binocular field is 18° wide, while that of the predatory snapping turtle, *Chelydra*, extends for 38° (WALLS, 1942). The largest binocular fields amongst the birds are to be found in the raptores; the hawks, kestrels, and eagles have binocu-

lar fields alleged to be from 35°–50° in width (PRINCE, 1956) and the owl some 60° (WALLS, 1942), although the tubularity of the owl eye makes its effective retinal binocular field only some 40° wide (PETTIGREW, personal communication). The generality of this correlation provides prima facie evidence for the possibility of dealing with the variation of binocular field width on a common basis throughout the vertebrate kingdom. The theory of HARRIS, however, fails to account for the observations which support JOHNSON'S (1901) phylogenetic correlation, and upon cross-class comparison such puzzles arise as to why the width of the binocular field in the predatory crocodile is as narrow (25°) as that of the rabbit and smaller than in the ungulates.

A further difficulty with HARRIS' theory (1904) is that the majority of the primates, although possessing the widest binocular fields, are not predators. HARRIS was content to accept this apparent anomaly as related to the interconnected development of sight and the use of the hand as a prehensile organ:

> Binocular vision is clearly of great assistance in the accurate use of the hand for fine movements, which, in proportion to its specialisation as a fine and delicate instrument, has been accompanied by an increasing development of brain power

(HARRIS, 1904).

The evolution of binocular vision among the primates has subsequently tended to be treated in isolation from that of the other vertebrates. The importance of the eye-hand relationship was again taken up by ELLIOT SMITH (1912, 1928, 1930) and his school (WOOD JONES, 1926; LE GROS CLARK, 1934, 1962, 1970; HILL, 1972) whose general thesis, the *arboreal theory* (HOWELLS, 1947), is that the frontal-eyed, prehensile, extant primates have evolved from nonprehensile lateral-eyed precursors (LE GROS CLARK, 1970) under the influence of selection pressures arising in arboreal locomotion per se.

The frontal eye position and wide binocular field of the primates was initially regarded as a result of the change of emphasis from smell to vision during primate evolution, of general benefit in providing a large field of stereoscopic vision (WOOD JONES, 1926), but simply a consequence of the recession of the snout (ELLIOT SMITH, 1912; WOOD JONES, 1926). The view that the wide binocular field and stereoscopic vision are adaptations for the accurate judgement of distance during arboreal locomotion (COLLINS, 1921) was adopted subsequently (ELLIOT SMITH, 1924).

Nevertheless, HAINES (1958) has pointed out that although the primates show structural specialization for the arboreal habitat, there are few such gross changes amongst the *arboreal* carnivores:

> ... the Indian mongoose *Herpestes mungo* is an accomplished climber, and takes readily to trees, but is structurally very similar to the terrestial *H. ichneumon*. The pine marten, *Martes martes*, can run down a squirrel leaping through the canopy and walk down a tree head first, yet its hands and feet show little difference from a terrestial polecat *Mustela putorius* ...

In a similar vein CARTMILL (1972, 1974) argues that the grey squirrel is the equal of a saltatory lemuroid in its arboreal agility, and yet its orbital convergence, optic axis divergence and manus evince no sign of primatelike change relative to the more terrestial ground squirrel. In fact, the majority of tree-dwell-

ing species do not converge with the primates in anatomic specialisation; *there are many different arboreal locomotory niches*, and the contrast between the primates and squirrels is alone sufficient contraindication of a common selection pressure arising in arboreal locomotion (CARTMILL, 1974).

In his *visual predation hypothesis* CARTMILL (1972, 1974) adopts WOOD JONES' (1926) view that grasping extremities arose not as adaptations to arboreal locomotion per se but for movement amongst the finest branches. In contrast to his expectation from the arboreal theory, he notes that orbital convergence is greatest in the slow, visually directed insect predators, such as *Loris* and *Nycticebus* which employ their grasping hand to take prey, rather than in the swift acrobatic species. Similar orbital convergence, after allometric correction, is reported for the marsupial manual insectivores *Cercatetus* and *Burramys* (CARTMILL, 1974). The increased orbital convergence of these manual predators is regarded (CARTMILL, 1972, 1974) as an adaptation of similar significance to that in other hunting species, such as cats, and taken to imply an increased field of stereoscopic vision. By analogy, therefore, CARTMILL suggests that the prehensile hands, frontal eyes, and, implicitly, the large binocular field of extant primates arose from a common ancestral form which inhabited the fine branches of the canopy and undergrowth of the tropical forests and employed its grasping hands for visually directed manual predation on insects and other prey.

Such primate precursors would be consistent with HARRIS' (1904) theory of predation as the "fount" of binocularity, but the problem of the nonpredatory frugivorous primates is simply evaded. CARTMILL (1972, 1974) has made no attempt to demonstrate the correlation, which is necessary to his hypothesis, between the binocular field width and the degree of orbital convergence; the binocular fields of nonpredatory primates appear to be as wide as those of predatory forms, and it is this, not the degree of orbital convergence, which is of functional significance. Indeed, in criticising the limited evidence for CARTMILL'S hypothesis SZALAY (1975) has pointed out that the most convergent orbits amongst the Malagasy strepsirhines are to be found in the phytophagous, forearm-dominated *Palaeopropithecus*. The retention of convergent orbits in this form and in extant phytophagous primates clearly indicates that visually directed manipulatory habits could be argued to provide teleologic justification for their evolution without any intermediate stage of visual predation.

An uncommon question: What functional advantage is gained by a wide binocular field? It would not in general be accepted that the advantage of the wide binocular field is that it simply

> affords a double assurance of information pick-up in a wider angle of the field ahead

(GIBSON, 1966), although this is to some extent true under quantum-limited scotopic conditions. Neither does it appear that the binocular field width of a given species correlates with the speed attained in normal locomotion. The 25° binocular field of the racing pigeon, which is typical of a granivorous bird, is thus markedly smaller than the 40°–60° of the hawk, although both forms are recorded as attaining air speeds in excess of 60 m.p.h. and even higher ground speeds; the binocular field of the slow-moving owl is similar in size to that of the swifter hawks. The binocular field of the slow loris is double the magnitude common in

ungulates which may attain speeds of up to 60 m.p.h. During smooth forward locomotion, adequate stereoscopic coverage of a much wider range of space than that to be entered by the body is provided by a relatively narrow binocular field; progressive change of course is accompanied by a gradual realignment of the binocular field towards the destination. It has been suggested that the irregular paths of swift predators engaged in the chase may put a premium on a wide binocular field in order that knowledge of the spatial organisation of the *environment* is immediately available during massive readjustments of the direction of movement. However, momentary consideration indicates that the prey lead the chase without apparent inconvenience, although commonly possessed of only narrow binocular fields. CARTMILL (1972) has suggested more specifically that cats and prosimians are better able to compensate for the evasive movements of their prey because of their wide field of stereoscopic vision. There is undoubtedly some truth in this argument even when applied to the *relatively* wider binocular fields of fish and reptilian predators rather than to extremely frontal species, but it is unsatisfactory as a fundamental explanation. In spite of wide binocular fields in the prosimians, the ballistic "smash and grab" technique of insect capture in *Galago* takes little account of prey movement (BISHOP, 1964), and stalking by neither *Loris* nor *Nycticebus* disturbs the prey until the hand touches it; compensation for flight reaction is not made in any of these prosimians, and the unitary prehensive pattern is readily disrupted (BISHOP, 1964). The *Tupaioidae* are able to grab flies in a similar fashion (LE GROS CLARK, 1927; POLYAK, 1957), in spite of a much narrower binocular field. Again, this explanation fails to account for the retention of the wide field in nonpredatory primates.

Such ad hoc explanations for the extent of the binocular field in a given species hinder the isolation of a common underlying function. According to DUKE-ELDER (1958), the wide binocular field simply provides stereopsis over a more extensive range of visual space than a narrow field; its application must be varied and very general:

> the extent of binocularity, on the other hand, is determined by the greater value of the fine judgement rendered possible by binocular vision in pursuit and attack by the predator, in its ordinary activities by the arboreal animal, or by the Primate the eyes of which have become accurately correlated with the use of its hands.

In the classic analysis, as summarised by WALLS (1942), the quality of "solid" vision in stereopsis is seen to be of some benefit in all species, so that there is a "*universal* urge to binocularity." The width of the binocular field attained by any species follows passively and inversely upon its need for panoramic vision. No specific adaptive significance is seen in the correlation between predatory or arboreal life styles and the presence of the wide binocular field; the wide field is expressed because of the low pressure for panoramic vision in these niches.

LINDSAY JOHNSON'S (1901) observation that there is a phylogenetic trend towards wider binocular fields is true in the sense that the mean width of the binocular field for a given class appears to increase from the fish to the mammals; within a class, however, the range is wide, and there are both fish and primates which possess binocular fields more than 100° wide. In the context of the classic analysis this would require that the importance of the panoramic field decrease throughout the phylogenetic series rather than that the importance of the binocu-

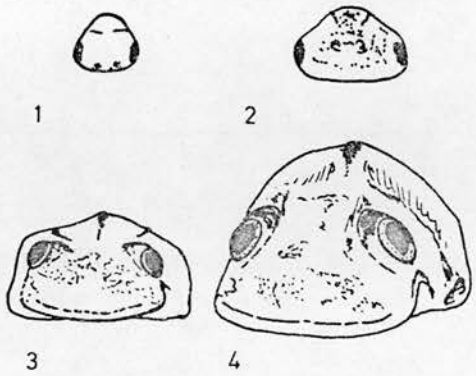


Fig. 4. Shift of eyes from their lateral position in *Xenopus laevis*, stage-46 larva, *1*, stage 48.2, to their more frontal location in the 20-mm-long juvenile, 3, and 34-mm-long juvenile, 4. (after R. M. GAZE, 1970)

lar field increase. An appropriate functional basis for the absolutely narrow binocular fields of fish and reptilian *predators* would thus be their common lack of effective brood care, independent lives when small (MITCHELL, 1912), and vulnerability to secondary carnivores when adult. The premium on panoramic vision would be greater for such forms than for bird and mammalian predators, which tend to lead a sheltered life when young.

The crocodile is a good case in point. It has been estimated that the survival rate of crocodiles to maturity is only 1% (STEVENSON-HAMILTON, 1912), compared to about 30% for the lion, in spite of an agressive nature at hatching and considerably more parental supervision than received by the majority of poikilotherm young; the majority are eaten by birds, cats, and other crocodiles. The surprisingly small 25° binocular field of the voracious and nearly invulnerable adult might thus be determined by its needs when immature.

The generality of this explanation is made suspect by the fact that the young of most *predatory* fish or reptiles are subject to the same degree of predation and cannibalism as their prey, or the young crocodile, and yet their binocular field may substantially exceed that of the adult crocodile in width, for instance, it is 40° wide in the pike (KAHMANN, 1935). It seems rather that the life style of the crocodile sets a low premium on a wide binocular field; stereoscopic vision necessary for its rapid forward lunges towards prey would be adequately provided by the narrow binocular field, and the animal appears to exploit its wide panoramic field to detect adjacent prey which are taken with a side sweep of the head and jaws which requires little judgment of depth.

Again, it is hard to believe that the adult frog or toad is less vulnerable than a young crocodile, and yet both forms surrender the advantages of panoramic vision at metamorphosis when the eyes rotate forward to give rise to a wide binocular field with a complementary blind area to the rear of the head [Fig. 4 (GAZE, 1970) and Fig. 5a].

Such instances make it impossible to accept WALLS' (1942) concept of a uniform universal urge to the development of a wide binocular field. Among the mammals it is obvious that the width of the binocular field may vary to some

extent independently of panoramic field width; the cat and primate binocular fields are significantly different, at 100° and 130°–140°, respectively, in spite of almost identical optic panoramic fields. It is thus concluded that *the relative width of the panoramic and binocular fields is determined by the interaction of separate selective pressures which are not universal in intensity but predominate only in certain lifes styles.* The wide binocular field of the frog thus fulfills some specific need which is not shared by the crocodile. It remains to specify in more detail just what aspects of a species life style determine the pressure for a wide binocular field; it is clear from the differing widths of the frog and crocodile binocular fields that it is not simply predation per se.

Praxic space and binocular field width: a systematic survey.

> There is the Yak, as great as a cloud shadowing the sky. Big as it is, it cannot catch a mouse.
>
> CHUANG TSU: Inner Chapters

The class of *visually* controlled activities involved in directed locomotion, prey capture, nest building, and other manipulations of the environment have been described as *praxic* behaviour (TREVARTHEN, 1968). Almost any part of the body may be employed for praxic activity; the horse kicks accurately with the rear legs or the crocodile sweeps prey into the water with a blow from its tail, but such instances are exceptions in the behavioral repertoire. In vertebrates such visually controlled actions are confined to a limited anterior segment of the egocentric behavioral space which, with the head in the primary position, is symmetrically disposed about the midsagittal plane and may be described as the *central praxic field.* The extent of this field is determined by the nature of the individual species' manipulatory organs and by the manner in which they are employed; its limits would be delineated by the locus beyond which reorientation of the body preceeds manipulation, directed activity, or a strike.

This section investigates the possibility that the width of the binocular field increases pari passu with that of the central praxic field. It is obvious that much of praxic behavior requires judgment of relative distances such as is provided by binocular stereopsis; during complex activities, depth information may be simultaneously required at several points in the field of view so that the more extensive the praxic range, the more a wide binocular field might be of assistance. This attempt at a general synthesis of the systematic data does not presume the width of the binocular field to be determined by one factor. Quite apart from the use of space by a given species, it is obvious that reliance upon scotopic vision also leads to a wide binocular field.

The recent revision of long-accepted measurements of the binocular and panoramic fields in common forms such as the cat suggests that the comparative literature contains many errors; the discussion of comparative aspects of binocular field width should therefore currently be based upon gross differences alone. This requirement is sustained by the fact that functional interpretation of binocular field width is implicitly couched in terms of the behavioral binocular field but at present is necessarily, although improperly, supported by reference to measurements of the optical rather than the retinal field.

Fish do not possess prehensile organs and

> on the whole are rather conspicuous for the lack of ability to manipulate inanimate objects

(THORPE, 1963). Tasks such as nest building are carried out by mouth so that the praxic field is little more than a strip of space running forward from the head. The binocular fields of this class are correspondingly narrow, rarely exceeding 40° in width; the limited extent of the 14° binocular field in the archer fish should not be surprising, as it was to KAHMANN (1935), because the animal always orientates so that its shot is directed along the midsagittal plane and is thus served by the narrow field. The extreme parallelism of the optic axes and frontal situation on the eyes in some deep sea fishes (WALLS, 1942; DUKE-ELDER, 1958) is misleading if interpreted as signifying a wide behavioral binocular field because of the restrictions set upon the retinal extent by the tubular form of the eye. A very

wide 120° overhead binocular field and substantial frontal binocular field have been described for the bullhead (POLYAK, 1957), but this is a predominately scotopic, nonvisual form, and the extensive binocular overlap is most likely an adaptation for increased sensitivity such as is found in certain mammals.

The development of forelimbs among the reptiles is not accompanied by an increase in the extent of their praxic space. *Chelonians* such as the snapping turtle may hold down food with the forelimbs while eating but,

> generally speaking, however, the limbs of existing reptiles play little if any part in the capture of food. The head is the main instrument of predation ...

(BELLAIRS, 1969) just as in the fish. Usually the prey is not stalked but waited for by the motionless reptile.

> Capture of agile prey is finally effected by a lunge or strike, or sudden rush culminating in a snap

(BELLAIRS, 1969). The central praxic space of these forms, like their binocular fields, is very narrow. Even in the anole and chameleon, which have wide-ranging eye movements and good depth judgment, the binocular field is relatively narrow. As among the fishes, it is the predatory species which have the widest binocular fields, especially when given to the sessile expectation of prey and attack by rapid lunges such as are employed by tree snakes and long necked turtles. The need for judgment of angled strikes without a revealing reorientation of the body and eyes, as well as for the guidance of head and jaw position during the impressively swift attack (FRAZETTA, 1966), could be understood to set a premium on a wider field of steroscopic vision in these forms, but its magnitude rarely exceeds 40°.

The 100° binocular field of the frog or toad is wide in comparison with those of the majority of vertebrate species and singular amongst the poikilotherms. This greater width is not accompanied by the use of the forelimbs for prey capture, although food may be held in the mouth or ejected by manipulation, nor is it associated with a more pronounced noctural component in the habits of these amphibians than evinced by more lateral eyed poikilotherms. The frog and toad are distinguished, however, by an extensive praxic space which arises from their leaping to prey over a 100° wide "jump-and-snap zone" without reorientation before attack (Fig. 5a) (INGLE, 1970); the width of the binocular field approximates this zone. The initial judgment of prey position must be especially accurate in the frog because its eyes are partially withdrawn during the leap, and visual feedback is eliminated (Fig. 5c). It remains puzzling why the binocular field is not better expressed in some fish, such as the mud-skipper, whose sessile predatory activies resemble those of the frog (MUNK, 1970) but whose binocular field is not more than 40° across (WALLS, 1942).

Although measurements are not plentiful, it appears that insectivorous birds which pursue prey with rapid darting adjustment of flight, such as swifts and swallows (POLYAK, 1957), possess binocular fields which are wide relative to the granivorous forms (WALLS, 1942). In spite of their subjection to greater brood care than is common amongst the poikilotherms, the birds do not reveal a tendency towards substantially increased binocular field widths. It is noteworthy that the largest fields are encountered amongst these raptorial forms which take their prey with two talon-equipped feet. The victim is fixated during approach, and the relative position of the feet with respect to it judged within the peripheral binocular field (Fig. 5m). The increased angular range of nearby praxic space which results from the use of the feet as well as the mouth during predation is thus again correlated with a wider binocular field, but it apparently extends for only some 40°–60°, even amongst the owls and hawks (WALLS, 1942; PRINCE, 1956; DUKE-ELDER, 1958).

The release of the forelimbs from purely load-bearing functions among a great variety of mammalian forms, including rodents, marsupials, carnivores, and primates, gives rise to the potential for more complex manipulative activity and increases the volume of local space in which praxic behaviour is possible. In contrast to the submammalian classes, the simple manipulation of food is carried out by many nongrazing mammalian species; rats will handle grain and other objects (BARNETT, 1963) and have in common with the *sciurids* the bimanual holding of food (POLYAK, 1957). A great variety of skill is revealed in the use of visually directed manipulation during killing and feeding among the dasyurid marsupials, insectivores, and carnivores (EISENBERG and LEYHAUSEN, 1972). In general, the frequency and complexity of such behaviour is related to the extent of grasping ability in the forepaws as well as pronative and supinative ability in the forelimbs. Such attributes are commonly correlated with arboreal skill so that among the *Viverridae* those species which employ the forelimb to pin down prey

Fig. 5. Instances of praxic activity which are discussed in the text

for the kill and feeding are highly arboreal, while those which rarely pin their prey and never hold food are highly digitigrade with little forelimb flexibility (EISENBERG and LEYHAUSEN, 1972). But even among the cursorial carnivores, the forelimbs always function as more than simple props (EWER, 1973). In parallel with this increase in the extent of praxic space, the binocular field widths encountered in this group are much greater than among herbivores and extend from 60° to 130°.

Only among species equipped for extensive abduction and adduction of the forelimb, and thus commonly demonstrating some degree of arboreal skill, is access to the widest range of manipulative space made available. The use of this range of space under visual control would alone be expected to lead to the development of a wide binocular field. According to the praxic space hypothesis, therefore, neither arboreal nor predatory habits lead per se to the widening of the binocular field, but this occurs because of the increased range of praxic behaviour common to *some species* pursuing these and other life styles. Unfortunately we have not sufficient information to examine the validity of the hypothesis in a wide variety of species and must deal only with certain obvious instances.

Consider dogs and cats. The dog has, as an endowment of its cursorial origin, only limited ability to rotate the forelimbs or grasp with the paws (EDEY, 1968). Such space to which the forelimbs have

access is simply not employed for praxic or even manipulatory activities. The *Canidae* kill small prey with a relatively undifferentiated thorax bite, shaking and tossing (Figs. 5d, e) (FOX, 1969); large species are dealt with by repeated crushing and tearing bites. The only use of the paws is to restrain, and occasionally strike, small prey before the kill and to hold the carcass when eating. In association with the limited praxic behaviour, we find the binocular field of the dog to be markedly smaller than that of the cat and to range in general from 70° to 80°: dingo, 70°, cocker spaniel, 80° (personal observation), and greyhound, 80° (PISA, 1939). Larger fields have been reported for some domestic forms (PISA, 1939), but these are usually "sports" of brachycephalic appearance subject to human fancy breeding.

By contrast, however, the *Felidae* combine visually directed behaviour over a wide range of local space with the most extensive binocular fields outside the primates. A few species of *Canidae* may approach the cat in the use of cover during visual stalking, but the *visually* directed killing bite is employed with unique precision by the *Felidae* upon even large prey. Visual direction of the bite towards the skull base is common to some marsupial carnivores and viverrids, but the characteristic felid kill (Fig. 5h), severs the spinal cord after two canine teeth have passed between the neck vertebrae (LEYHAUSEN, 1965). The precise location of this bite is uniquely aided by manipulation:

> it is only within the family Felidae that we find a definite selection favouring the use of the forepaws in restraining prey with a specialised clasping movement prior to the administration of a killing bite

(EISENBERG and LEYHAUSEN, 1972). The visual domination of the extensive manipulatory repertoire of the domestic cat is well known but is common to other Felidae; the leap by which birds or butterflies may be "fielded" with one or both paws (Fig. 5a) is a widespread example of such praxic behaviour (EDEY, 1968) and characteristically differentiates this family from the Canidae which employ the mouth to catch insects (ROMANES, 1882).

The singularly wide 100° binocular field of the domestic cat is thus seen as accommodating a variety and range of praxic behavior remarkable among subprimates. The combined use of the mouth and paws during the initial stage of an attack requires the simultaneous visual fixation of the neck of the prey and accurate but independent direction of the left and right forepaws. The extensive field of feline steroscopic vision is ideally suited to such a task.

A similar argument may be applied to primates which must accurately and independently locate their hands in the peripheral visual field while the eyes simultaneously fixate a goal during brachiation, leaping, clinging and an enormous variety of other focal praxic activities (Fig. 5i, j, k, l). The range of manipulatory and locomotory praxic space employed by carnivorous and frugivorous primates alike is greater than that of any other species of vertebrate and, in accordance with the praxic space hypothesis, is correspondingly found to be associated with the widest binocular fields of any species of animal.

It is curious that in spite of their quite narrow 60° binocular fields (LANE et al., 1971), the squirrel and tree shrew demonstrate considerable visually directed manipulative activity (see POLYAK, 1957); it is probable that the range of space accessible to the forepaws of these forms is relatively as great as in the cat. It is conspicuous, however, that both species, although essentially arboreal, spend a great deal of time on the ground surface, where they are particularly vulnerable to predators, and the need for extensive panoramic vision may result in restricted expression of the binocular field.

In order to differentiate the praxic-space hypothesis from the theory of the binocular field held by ELLIOT SMITH (1924), it is to be emphasized that the presence of the wide binocular field is now suggested to be correlated with an extensive range of praxic space and not with skilled manipulation per se. Thus BISHOP (1964) has suggested that racoons may be superior in manipulatory skill to prosimians, and the otter is equally dexterous (POLLOCK, 1921; MAXWELL, 1960, 1963), yet, from measurements made on photographs, neither of these animals appears to possess a binocular field greater than 70° wide; their optic axes diverge more than in dogs (JOHNSON, 1901). Both species have a wide range of manipulatory space, but the skilled use of the hand appears to have developed for rooting crustacea out of crevices by means of tactile cues in the absence of visual control (EDEY, 1968). Thus BLANQUART DES SALINES (BUFFON, 1812) described the racoon as dexterously opening oysters

> as well as all other of his operations, by feeling alone, seldom making use of either his eye or his nose.

The animal is nocturnal and fish are taken by touch (ERRINGTON, 1967).

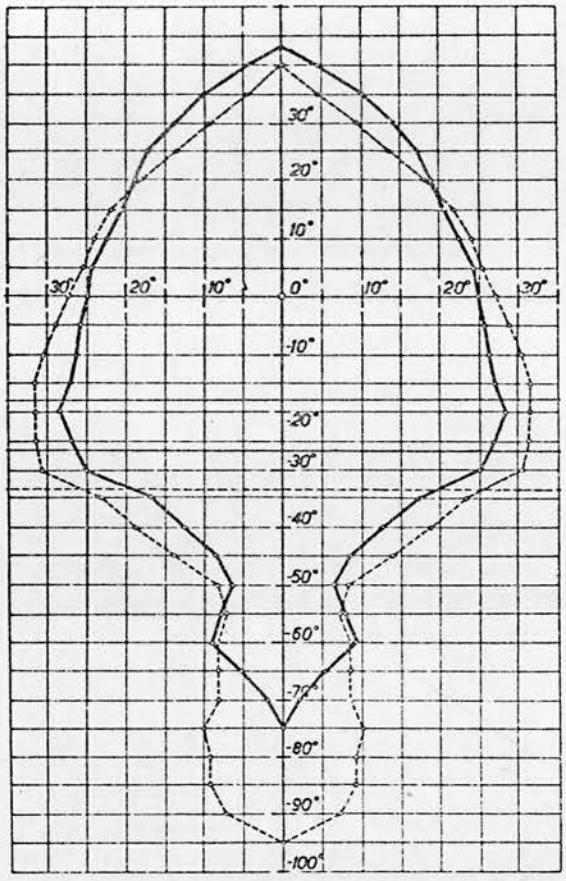


Fig. 6. The absolute *(hatched line)* and restricted *(bold line)* binocular fields of horse. Maximum width is about 55° at the equator; it attains a frontal elevation of 40° and declination of 75° to deal with ground near feet. This extensive inferior binocular field is reflected in the retinal ganglion-cell topography by presence of an anakatabatic region (Fig. 20) common to retina of other grazing species (PISA, 1939)

Although the otter usually hunts fish by sight, its praxic field is small during this activity, because they are captured by mouth (Fig. 5u); the forepaws are not employed until eating on land (EDEY, 1968; MAXWELL, 1960) (Fig. 5t); food is readily discriminated by touch in turbid water (EDEY, 1968). Such narrow binocular fields in species with well-developed tactile and manipulatory skills strongly supports emphasis upon praxic acitivity rather than manipulation as a primary factor in the determination of binocular field width. It might be suggested that these forms require panoramic vision to such an extent as to prevent expression of a wide binocular field, but the otter, at least, is not subject to significant natural predation (HARRIS, 1968), and such an explanation is unconvincing.

A more ambitious formulation of the praxic-space hypothesis might attempt to account for the shape of the binocular field, but that would be premature. It is worthy of note, however, that the binocular field of artiodactyls and perissodactyls is extended *not in width but downwards* along a narrow strip in the midsagittal plane, for more than 90° in the horse (Fig. 6), to deal with the limited region of space accessible to the nonabductable forefeet (PISA, 1939).

The assumption that a wide binocular field *necessarily* implies great emphasis on stereopsis is implicit in the surprise often encountered upon drawing attention to the 80°–100° wide fields of rat, mouse, and hamster. These preyed-upon species can be no less subject to pressure for an extensive

panoramic field than the tree shrew or squirrel, and yet, in spite of a much inferior range of praxic behaviour, their binocular fields are distinctly wider. It is notable, however, that these rodents also possess *overhead* binocular fields which are as wide as their frontal binocular fields. The continuous overhead coverage required to give warning of aerial predators could, however, be equally provided by the abutment of the upper margins of the two uniocular fields. It has been suggested (HUGHES, 1971) that uniocular field overlap in the upper binocular field of the rabbit, which is about 35° wide, ensures continuous coverage of the sky when the head is rotated and blocks off the field of one eye, but this explanation hardly suffices for the 100° wide overhead field of the rat or mouse. The small interocular distances and the low innervation densities of the retinal regions dealing with the upper field ensure that stereopsis within such an overhead binocular field would be very crude and appropriate to such short distances as to be of little use in the avoidance of aerial attacks. The most acceptable explanation of these very extensive fields of binocular overlap characteristic of nocturnal or, more generally, scotopic forms is that they simply increase sensitivity in conditions of low illumination. Such a conclusion does not, of course, preclude stereopsis within the frontal binocular field of these species.

Predation, arboreality, and manipulative skill per se have been rejected above as determinants of binocular field width. The range of visually directed praxic activity, not necessarily involving forelimb manipulation, and the need to exploit over a wide field the lowering of the luminance threshold obtained by binocular viewing have been suggested as alternate primary influences. Although the concept of a *universal* urge to binocularity modulated by the need for panoramic vision has been set aside, it is apparent that interaction between the pressures selective for the two fields must exist in certain life styles. However, even with only these three effective influences on the relative extents of the binocular and panoramic fields, it is found that the variety of possible explanations for the condition in a given species is an *embarras de richesse* which tends to make indulgence in them appear facile. But such attempts are justifiable if based on sound behavioral data.

Nevertheless, many hoary problems remain unsolved. Why do the nonsaltatory, cursorial, herbivorous forms such as the ox so greatly exceed even the nonmammalian predators in binocular field width when their limited manipulative skills are equally dependent upon specializations of mouth, teeth, and tongue, rather than on their nonabductable forelimbs, and they appear to be in similar need of protective panoramic vision? Why is the binocular field of the dog so large when it is obviously a species relatively deficient in visually directed manipulative skill and possessed of a restricted praxic field? Perhaps the greater extent of the cat binocular field should be accounted for in terms of specialisation of increased scotopic sensitivity rather than by emphasis on its skills! The best hope for a satisfactory future exposition of this subject clearly lies in the combination of accurate optic measurements, extensive behavioral studies in the natural habitat, and the techniques of numerical taxonomy.

The observations of CANELLA (1936a, b) indicate that monocular vision in all classes of vertebrates lacks any obvious qualitative deficit relative to binocular vision during everyday locomotion, jumping, or dealing with food. Monocular frogs (see INGLE, 1972, 1973), kestrels, and cats appear to be as capable as binocular animals in capturing their aerial prey. If the total loss of stereopsis and other binocular cues to depth, such as image size and binocular perspective difference (OGLE, 1950), is attended by so little apparent deficit in normal life, it is not surprising that the peculiar adaptive significance of the wide peripheral binocular field proves elusive.

An implication of the praxic-space hypothesis is that the peripheral binocular field is primarily organised to deal with nearby space. At present, stereoscopic vision has been studied in primates alone and then only at small eccentricities; little is known of the quality of fine judgment in the peripheral binocular field. Recent work by BLAKEMORE (1970) shows that over a 3° range of disparity bridging the fixation point, there obtains a sensation of depth proportional to the displacement of an object from either the fixation point or another object within this range; the region, although more extensive than was originally conceived

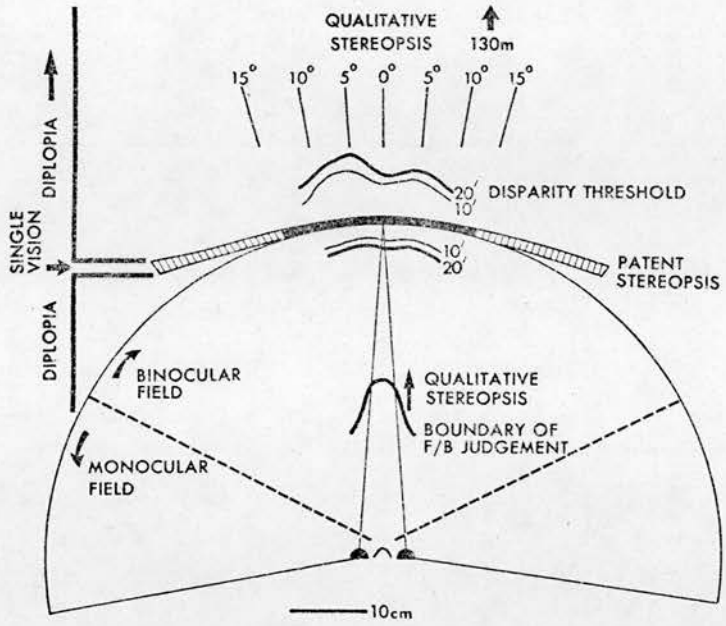


Fig. 7. A diagrammatic horizontal section through human binocular field which summarizes spatial distribution of the various qualities of stereopsis for a given degree of vergence. It is emphasised that depth judgement is not confined to the region of patent stereopsis. The lack of information about peripheral stereopsis is clear. [Compounded from the data of OGLE (1950), FLOM (1957), and BLAKEMORE (1970)]

(OGLE, 1950), is described as providing *patent stereopsis*. As shown in Fig. 7, vision within this range may be single or diplopic; outside it extends the area of *qualitative diplopic stereopsis* in which fore/aft judgments of depth relative to the fixation point may be made without relative depth sensation. The distribution of stereoacuity and patent and relative stereoscopy at eccentricities greater than 16° from fixation has been little studied, but Fig. 7 combines the results of three workers (OGLE, 1950; FLOM, 1957; BLAKEMORE, 1970). It is generally agreed that, although stereoacuity decreases in the peripheral binocular field, the range of patent stereopsis increases. If peripheral stereoacuity continues to be proportional to visual acuity (OGLE, 1950), then from WERTHEIM (1894) and BLAKEMORE (1970) we would estimate that from 0.4′ at the fixation point it will drop to some 15′ on the horopter at an eccentricity of 50°. The spatial displacement represented by this threshold would vary with the angle of vergence of the eyes, but during fixation at 50 cm it would represent about 5 mm at an eccentricity of 50°. Although obviously much cruder than central stereopsis, the peripheral binocular field of man thus has the potential for making the quite fine spatial judgments attributed to it by DUKE-ELDER (1958).

For other species nothing is known concerning the quality of peripheral stereopsis, but neurophysiologic results from the cat are compatible with the suggestion that the animal possesses a PANUM's fusional shell similar to that in man (JOSHUA and BISHOP, 1970). A recent investigation has shown PANUM's area to be

some 50′ wide for crossed disparity in the cat, compared with 10′ in man, but the range of qualitative stereopsis, unlike that of man, is not much greater than that of fusion (PACKWOOD and GORDON, 1975).

4. Frontal Vision

The eyes of the Primates and Felidae are described as frontally situated; this is a loosely defined tripartite syndrome involving a small divergence of the optic axes, the absence of a panoramic field to the rear of the head, and, as commonly understood, a wide binocular field. A satisfactory explanation of frontality would encompass all of these features, but for many writers the implicitly associated wide binocular field simply,

> provides an essential basis for stereoscopic vision

(LE GROS CLARKE, 1962), and the frontal condition requires no further explanation.

This view may be traced back to ELLIOT SMITH (1928, 1930) whose still-current hypotheses (LE GROS CLARKE, 1962; HILL, 1972; SPATZ, 1968) have dominated primatologic thought on the evolution of binocular vision for the last half-century in spite of their inadequate experimental basis. For ELLIOT SMITH, binocular vision is acquired only at the level of the cat or monkey; the presence of the frontal eyes enables "macular" vision of unique quality, and stereoscopic vision is possible only after the attainment of macular vision (ELLIOT SMITH, 1928, 1930). With these features the vision of man and the higher primates, the "New Vision," is unique amongst all the animals,

> a vision of the world was thus revealed to man, with an appreciation of form, colour, size and space and a fuller understanding of distance and movement

(ELLIOT SMITH, 1930). But the argument of this chapter is the antithesis of his view. Binocular vision is assumed to be universal among mammals, the common mammalian area centralis is argued to have the potential for all the attributes of macular vision, except its high resolution, and stereoscopy is suggested to not justifiably be regarded as absent from any mammal possessing a binocular field; the vision of primates is not qualitatively different from that of many subprimates. If therefore, all of ELLIOT SMITH'S envisaged advantages of frontality are already in the possession of nonfrontal precursors then the evolution of frontal vision requires a justificatory basis different to that generally proposed.

It cannot be accepted that frontality may be equated with the acquisition of a large binocular field; the owl and some deep sea fish are undoubtedly frontal species, but their binocular fields are quite narrow because of the tubular structure of their eyes. It is the parallelism of the optic axes and, equally important, the absence of the rear panoramic field which are diagnostic. It has been argued that the inherent limitation on the extent of the uniocular optic field makes the loss of the rear panoramic field inevitable in a species which acquires a large binocular field. This might be valid for species with tubular eyes but is quite inappropriate for man or cat, because both forms fail to exploit some 30° of their uniocular optic fields. Any explanation of their frontality should encompass this fact.

The convergence of Primates and Felids in their development of frontal vision was regarded by HARRIS (1904) as not so much directed towards increase in the extent of the binocular field as arising from the common need for predators and manipulators to ensure that

> the two maculae are brought to bear on the same object.

This erroneous belief is founded on the still-encountered equation of the optic and visual axes. JOHNSON (1901) writes of man and monkey *alone* as possessed of "parallel vision" when the eyes are in the position of rest. Divergent optic axes are understood as implying divergent areas of good vision. Of course, it is now generally realized that the optic axes have not been found to be parallel in any species. Universally among investigated mammals there is substantial evidence that a subregion of the area retinae, the visual pole (BISHOP et al., 1962), receives the image of a distant point in both eyes simultaneously subject to the error introduced by small, dissociated, involuntary eye movements. Effectively parallel fixation axes are thus compatible with widely divergent optic axes. The situation during the observation of nearby objects is dependent upon whether the species is capable of vergence, but this has so far been unequivocally demonstrated only for primate and cat (HUGHES, 1972).

It remains possible, however, that frontality arises in man from a need to bring both *optic* axes to bear on the same object! The results of CAMPBELL and GREEN (1965) indicate that optic attenuation significantly limits the human contrast sensitivity for high spatial frequencies imaged at the fovea. Because the human eye resembles a Gaussian system to the extent that its image quality deteriorates with increasing eccentricity from the optic axis (see WEALE, 1956), it follows that the neural potential of the fovea to achieve low-contrast sensitivity thresholds at high-spatial frequencies would ideally be optimal upon fusion of the visual and optic axis; in man they diverge by only 6° (HELMHOLTZ, 1924). If the achievement of such fusion is the primary adaptation in frontality, the fabric of the optical and neural apparatus remaining unchanged, then restriction of the panoramic field to the rear of the head follows as a necessary consequence. The temporal optic hemifield of the human eye, defined by the 98° angle between the limit of the uniocular optic field and optic axis in the horizontal plane (HELMHOLTZ, 1924; HARTRIDGE, 1919), is as large as encountered in any mammalian species. Increase of the temporal hemifield to encompass the rear field could only occur with lateral rotation of the optic away from the visual axis and consequent loss of image quality at the fovea.

This explanation of frontality is probably as applicable to the remaining foveate Simians as it is to man, but its general validity might be questioned in relation to the Prosimians and cat, because their low ganglion-cell density, high receptor-to-ganglion-cell-convergence ratio, and lack of a fovea (ROHEN and CASTENHOLTZ, 1967) suggests that optic attenuation may be much less significant to central resolution than in Simians. However, measurements of optic quality available for the cat show that two necessary requirements for the applicability of the above hypothesis may be met. Not only is the optic quality of the cat eye reported to be maximal close to the optic axis (BONDS, 1974), but also the resolution of high spatial frequencies appears to be significantly limited by optic factors—although

the situation remains open to discussion. Sufficient information is not available to discuss the relevance of this explanation of frontality to the owl and deep sea fishes. It should not be too readily discarded for these species; the owl (FITE and ROSENFIELD-WESSELS, 1975) and at least one deep sea fish (WALLS, 1942) possess a fovea, a structure usually associated with high-resolution vision of such quality that oblique imagery may be undesirable.

C. Comparative Optics

I. The Schematic Eye

1. Introduction

Numerous optic, physiologic, and ophthalmologic problems involving the passage of light through the eye may only be solved by means of a quantitative model of the average dioptric system. Such a *schematic* eye enables the compound coaxial optic apparatus of the lens and cornea to be treated as a whole. A model human eye based on ray tracing was presented by YOUNG (1801), but an analytic treatment of the eye only became possible with GAUSS' exposition (1841) of the assumptions under which a compound system may be specified in terms of three cardinal points. For the human eye the early work of LISTING (1845) and HELMHOLTZ (1856, 1866, see 1924) culminated in GULLSTRAND'S schematic eye (1908). The descriptive mensuration of the animal eye began perhaps with NEWTON'S treatment of the sheep globe (ca. 1680; BREWSTER, 1860), in which the ellipticity of the cornea was first recorded (Fig. 8A); but attempts at an analytic optic treatment of species other than man awaited MATTHIESSEN (1879–1893) and HIRSCHBERG (1882); the provision and use of schematic eyes has, however, flourished only recently as a basic tool for neuro-ophthalmologic studies. In spite of an extensive qualitative literature on species differences in ocular organisation, the *comparative* quantitative study of dioptric systems remains relatively neglected.

The Gaussian theory contains certain assumptions—that light travels rectilinearly, is homogeneous, is incident close to the axis of spherical refracting surfaces arranged coaxially and separating homogeneous media—which are untrue and set varying limitations on the adequacy of a schematic eye as a model of the real dioptric system. The visual axis of man is sufficiently close to the optic axis for rays which reach the fovea to be regarded as paraxial and their course determined from a Gaussian schematic eye. The greater divergence of the optic and visual axes in most other species means, however, that the optic path described by an axial schematic eye is not appropriate to the retinal area of best vision, and its usefulness is therefore much reduced. The improvement of schematic eyes to embrace marginal and oblique rays poses formidable theoretical and computational difficulties, yet it is probably true that some of the most interesting contrasts in optic organisation between species will be encountered in the mechanisms for imaging from marginal and oblique rays. It may be that the inherent limitations of the Gaussian approach has discouraged its more general application, but it is surprising that schematic eyes are available for so few species in spite of the fact that interest in such models was well developed by the middle of the last century.

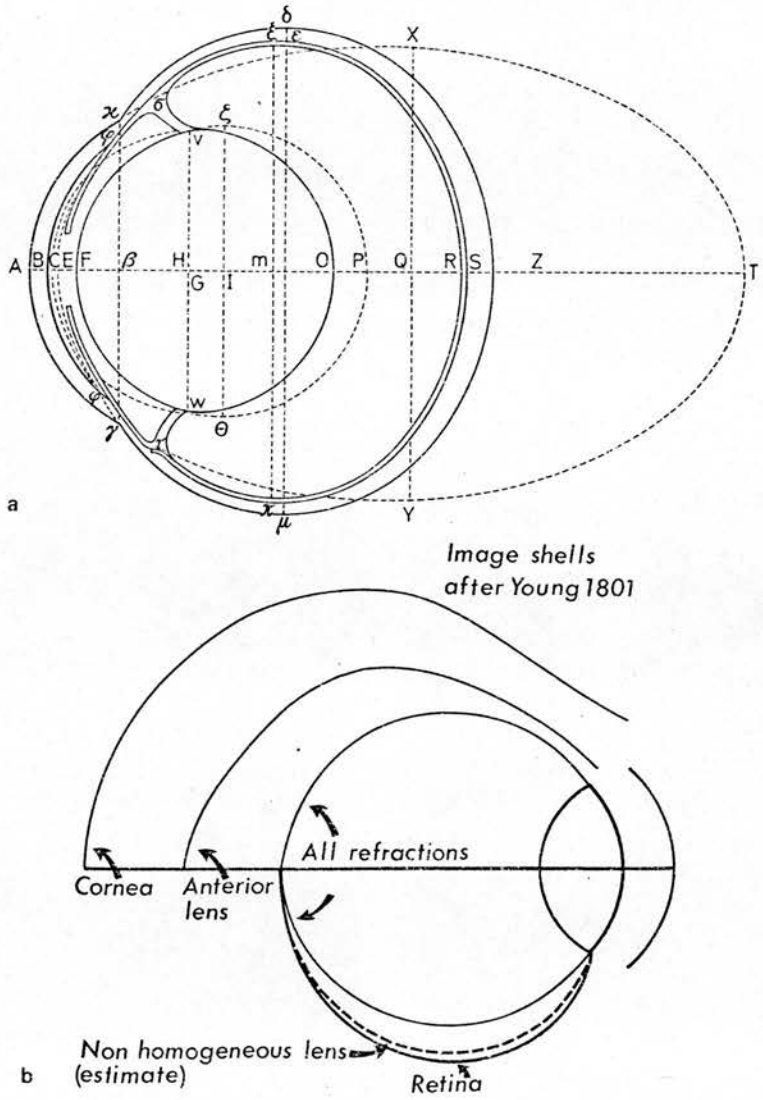


Fig. 8(a). Newton's schematic diagram of the sheep eye in which the ellipticity of a cornea was first described. Earliest known quantitative description of the optics of an eye (BREWSTER, 1860). (b) THOMAS YOUNG's schematic cross section of human eye, illustrating image shells obtained by calculation of net refraction achieved by successive surfaces in the dioptric apparatus. He recognized the presence of oblique astigmatism and, in assessing the influence of nonhomogeneity of lens refractive index, did not bring the final peripheral image shell into conjunction with the retina. (After YOUNG, 1801)

2. Methods

The essential purpose of a schematic eye calculation is to locate the cardinal points of a complex optic system. These comprise the primary and secondary focal points, principal points and nodal points which, between them, uniquely determine the behaviour of paraxial rays. For a *thin lens* the optical centre acts as

principal and nodal points, and its separation from the focal points defines the focal length of the lens. A *thick lens* or *reduced equivalent system* behaves for incident rays like an equivalent thin lens placed at the first encountered principal point and for emergent rays like the same thin lens placed at the subsequent principal point; focal lengths are thus defined for such a system in terms of the principal points rather than an optical center. If the refractive index of the first and last media of the system is not the same then, as in the eye, a ray which enters the first principal point does not leave the second principal point at the same angle to the optic axis; under these conditions that property belongs to the nodal points. The separation of the posterior nodal point from the posterior focal point, the posterior nodal distance or PND, is therefore a very important parameter in visual neurophysiology, because it defines both image scale and surface curvature.

It is possible to straightforwardly determine the three posterior cardinal points after measurement of the refractive error, vitreous refractive index, and PND of an eye. The PND may be obtained from measurements of the transclerally viewed image of an object of known angular dimension (VAKKUR et al., 1963) or somewhat more satisfactorily from the angular dimensions of fundus features of known size (HUGHES, 1976a). So far, however, the cardinal points derived this way have been employed only to confirm those based on calculation from the position and curvature of the refractive surfaces of the eye (VAKKUR et al., 1963; HUGHES, 1976a).

The computation of a complete schematic eye begins with the use of thick-lens theory to develop equivalent lenses for the cornea and crystalline lens. It is finished when a further equivalent lens is derived by combination of the equivalent corneal and crystalline lenses to represent the behaviour of the entire optic system. The theoretical basis of the computation is presented in this handbook by WESTHEIMER (1972b) and more extensively by GULLSTRAND (1924) and DUKE-ELDER (1970); SOUTHALL (1964) provides a convenient computational paradigm.

The calculation of a schematic eye requires knowledge of the position and radius of curvature of each refracting surface and the refractive index of each of the media in the modeled globe. These parameters should ideally be obtained from the living eye with an intact circulation; however, in spite of the availability of suitable techniques (HELMHOLTZ, 1924; SORSBY et al., 1957; DUKE-ELDER, 1970), current human and other schematic eyes are based upon measurements of enucleated and dissected globes. Changes in the dioptric components during growth have, however, been followed by such in vivo methods in rabbit (LUDLAM and TWAROWSKI, 1973) and children (LUDLAM et al., 1972). For optimal results the necessary parameters should be measured and a separate schematic eye computed for each globe studied (VAKKUR and BISHOP, 1963), averaging being only subsequently carried out on the parameters of the equivalent optic systems. The majority of schematic eyes are, however, computed from averaged data and are thus somewhat less satisfactory. The availability of the dimensions and positions of the dioptric components of the eye enables a great variety of optical calculations including estimation of the field of view, entrance and exit pupils, contact lens form, etc. The full schematic eye with extensive measurements of the globe components is thus more useful than a simple knowledge of the cardinal points of its equivalent dioptric system.

A common method for obtaining the necessary measurements has been to photograph rostral views of the globe and lens immersed in saline after enucleation (VAKKUR and BISHOP, 1963), but in other instances (HERMANN, 1958; SUTHERS and WALLIS, 1970), measurements were made on photographs of the globe hemisected after rapid enucleation and freezing. In both techniques the excised eye should be subject to an internal hydrostatic pressure similar to that in life (25 cm H_2O), but there is a great risk of distortion or displacement of the lens if a cannula is introduced into small eyes. Freezing, on the other hand, may disturb the relative positions and dimensions of the optic components of the eye upon volume expansion of the vitreous by about 9% (FISCHER, 1907; HUGHES, 1975b).

When measuring a small globe for the computation of its schematic eye, it is worth taking note of the extraordinary accuracy that is required if the original refractive state is to be reconstructed. In a 6 mm diameter eye such as that of a rat, an uncertainty of 0.05 mm in the separation of the focal and receptor planes is equivalent to an indeterminacy of the refractive state of about 1 D. Even with great care some dimensional uncertainty remains, e.g., the thickness of the choroid when full of blood may not be known so that the receptor plane cannot be accurately sited in the model (VAKKUR and BISHOP, 1963).

The measurement of the refractive index of the fluid media is straightforward when an Abbé refractometer is employed, and the results of VALENTIN (1879a,b) and FREYTAG (1910) remain representative. The disruption necessary when taking samples of the lens and cornea for use in such an instrument might be thought to be a source of considerable error, but the refractive index of any specific region of the lens appears to be determined entirely by the local protein concentration (PHILLIPSON, 1969). The examination of local samples in the Abbé refractometer gives similar values to more sophisticated techniques. In most schematic eyes the need to measure the lens refractive index is avoided as described below, but in more ambitious models it is necessary to obtain the description of the refractive-index variation across the plane containing the anteroposterior axis of the lens—the isoindicial equation. With assumptions, such a curve may be fitted to local samples (HELMHOLTZ, 1924; it may be obtained by a scanning refractometer (rabbit, NAKAO et al., 1968; cat, monkey, man, NAKAO et al., 1969) or computed from the protein-concentration profile established by microradiography (rat, PHILLIPSON, 1969).

The use of the dimensions of the excised lens generates an unaccommodated schematic eye for the rabbit, cat and rat because its shape is invariant during accommodation in these species. Frozen sections through the equator of the monkey eye would give lens dimensions for the unaccommodated state, but those obtained from the excised lens lead to an accommodated schematic eye (VAKKUR, 1967).

3. Choice of the Schematic Eye Model

An equivalent lens for the cornea is straightforward to derive, and its combination with the equivalent crystalline lens to form the schematic eye is readily achieved (SOUTHALL, 1964); it is the derivation of the equivalent crystalline lens which necessitates careful consideration and compromise. The difficulty arises, because the refractive index of the lens is not uniform throughout.

That the refractive index of the human and other crystalline lenses varies both radially and axially is a long-established fact. As early as 1801, THOMAS YOUNG extensively discussed the influence of this gradient in reducing the separation of the image shell and the retina as determined by ray tracing through the refracting surfaces (Fig. 8 B). BREWSTER (1816) employed polarized light to demonstrate the variation in optic density of the lenses of various species. Both YOUNG and BREWSTER were aware of the potentiality of the gradient for reducing aberrations, but quantitative treatment was not possible in the absence of its analytic description. Stimulated by the examination of the fish lens, MAXWELL (1854) demonstrated that perfect imagery would be possible in a medium in which the refractive index varied inversely as the distance from a given point, but only if the object and image lay within the medium (MAXWELL, 1858). If a similarly organised lens were to be placed in a homogeneous medium, then, as demonstrated earlier by YOUNG (1801), perfect imagery was not possible, although some advantage in minimizing the aberrations would accrue from the gradient of index (FLETCHER et al., 1954) The effect of the gradient was clearly understood by YOUNG (1801) to make the lens more powerful than if it were uniformly constructed of material of the same index as the core (HELMHOLTZ, 1924).

One obvious solution has been to dispose of the refractive index measurements on the crystalline lens and to represent the lens by an equivalent organ of identical shape but of uniform and higher refractive index; this is the Gaussian homogeneous lens model which has been extensively employed for man (LISTING, 1845; HELMHOLTZ, 1924), cat (VAKKUR and BISHOP, 1963), rabbit (HUGHES, 1972), and rat (BLOCK, 1969; HUGHES, 1977c). It is to be emphasized that the effective, or *total* (SENFF, 1846) refractive index employed for the homogeneous lens considerably exceeds the actual values observed at the center of the crystalline lens core (HELMHOLTZ, 1924). Gross errors are introduced if it is replaced, as in MASSOF and CHANG's "revised" rat schematic eye (1972), by a mean index arbitrarily derived from actual measurements of the crystalline lens index.

The homogeneous lens is computed by a relaxation technique whereby its effective refractive index is chosen so that the back vertex power of the model and the crystalline lens are identical (VAKKUR and BISHOP, 1963; BLOCK, 1969). The principal points of such a lens model remain necessarily separated by a greater interval than those of the corresponding crystalline lens (HELMHOLTZ, 1924; GULLSTRAND, 1924), and the power of the homogeneous lens is greater. The misrepresentation of the principal points resulting from the use of the homogeneous lens in the cat schematic eye is small and introduces a refractive error of only 0.5 D (VAKKUR and BISHOP, 1963). In small eyes, such as those of goldfish or rat, the error arising from the use of a homogeneous lens may amount to 4 D, so that a more sophisticated model lens is required.

The refractive contribution of the lens to the schematic eye is made up of the sum of its normal surface contributions, additional surface contributions resulting from inhomogeneity, and the transfer contribution due to refraction by the intervening nonhomogeneous medium. It is the additional surface contribution and the transfer component, described as the core of the lens by MATTHIESSEN, which is problematic to represent in the schematic eye. Many authors attempted to use approximate laws for the variation in index across the lens (GULLSTRAND, 1924), but these were inadequate for a variety of reasons. MATTHIESSEN (1887) stated that the indicial equation for the lens of many species was such that the effective total index was as much greater than the refractive index of the crystalline core as the index of the core is greater than that of the cortex surface. Comparison of the total indices for cat, rabbit, and rat in Table 1 with the core and cortex values indicates the inadequacy of this model.

A substitute for the inaccurate homogeneous model of the human lens was presented by GULLSTRAND (1908; 1924) in the form of the *equivalent core lens*. To derive this model, GULLSTRAND approximated the human indicial equation along the optic axis by means of a series expansion. After indirectly determining the various constants, the power and principal points of the core lens were derived by integration. For representative purposes these properties of the lens core were then employed to define a unique *equivalent core lens*. This consists of a pair of refracting surfaces forming a homogeneous lens of refractive index equal to the crystalline lens center and regarded as suspended in a homogeneous medium of the same refractive index as that of the vertices of the crystalline lens cortex. The advantage of the equivalent core lens is that

> so far as the imagery laws of the first order are concerned the entire lens system then has precisely the optical characteristics of the actual crystalline lens

(GULLSTRAND, 1924). The principal points occupy positions exactly corresponding to those of the real core lens. A more recent seven-shell lens with aspheric vertices has been employed to simulate spherical aberration of the organ (LOTMAR, 1971).

In so far as all adult vertebrate crystalline lenses contain a central core of higher refractive index and density than the surrounding cortex, the equivalent core-lens model might be regarded as less arbitrary than the homogeneous lens. It must be realized, however, that the equivalent core lens is determined by calculation and not by anatomic demonstration—it does not have any exact physical counterpart and is simply a model of the real lens core or transfer component.

The in vivo state of the lens could not be determined for man by measurements on the excised organ because of the changes which occur in its form upon cutting the zonular fibres; GULLSTRAND (1924) thus derived the power of the lens from consideration of the aphakic eye. The stiffness of the cat, rabbit (FISHER, 1971), and rat lenses is too great for such a change of shape to occur upon their excision, so that their power may be directly determined by measurement of their vertex powers when suspended in saline. However, in spite of the availability of actual isoindicial, rather than approximated, curves for the meridional sections of lenses in a variety of species, there have been no derivations of core lens schematic eyes for forms other than man.

The availability of the isoindicial curves for the rat lens (PHILLIPSON, 1969) suggested the computation of a *two-shell* model lens in an attempt to overcome the shortcomings of the homogeneous lens for this small eye (HUGHES, 1976b). The central meridional isoindicial contours of the rat lens are circular in section and correspond closely to a real spherical core which may be extracted from the crystalline lens and is found to have a quite uniform and high refractive index. A two-shell model is thus well supported anatomically but is an approximation in that the cortex is treated as homogeneous. After specification of the core and cortex refractive indices in terms of the limiting values of the crystalline lens, then its spherical form means that only the equivalent core (or central shell) radius remains as a variable for matching the power of the two-shell lens to that of the crystalline lens. This model does not, of course, correspond to that derived by GULLSTRAND in that no integration of the indicial equation is employed, but it is an improvement on the homogeneous lens model and unique for a circular central shell. The two-shell rat lens model is less powerful than the homogeneous lens by 3.5 D, but in the complete schematic eye, the influence of the greater separation of the homogeneous lens principal points predominated over its greater power, and the refractive state is some 4.3 D more *hypermetropic* than that of the two lens shell schematic eye.

The isoindicial curves computed from the refractive-index gradient across the lens of various species have enabled NAKAO and his colleagues to attempt computer-ray trace models of the lens for the assessment of aberrations resulting from marginal incidence. Some 2000 shells were employed to approximate the continuous gradient of refractive index in the rabbit lens (NAKAO, 1968). Although an

important improvement in the methodology of this field, it is clear that problems remain, because the computed focal length of this lens is not in agreement with either that of the rabbit schematic eye (HUGHES, 1972) or the confirmatory results of LUDLAM and TWAROWSKI (1973); the flaw may lie in the freezing of the lens or in the computation itself. Two human schematic eyes based upon multiple shell lens models have been recently reported—one in brief (NAKAO et al., 1970), the other—with 98 shells—in more detail (POMERANTZEFF et al., 1971).

Simple geometric ray tracing is not adequate for the rigorous analysis of media with continuously varying refractive index. WOOD (1911) illustrated this by the fact that light initially travelling parallel to linear isoindicial contours undergoes a refraction towards the denser medium, which ray tracing would not lead one to expect. Numerical solutions of the differential equation which describes the ray path in inhomogeneous media have been developed (MARCHAND, 1970) but do not permit the contributions of the system components to be independently explored.

The problems encountered in the attempt to derive an accurate paraxial schematic eye thus result from the structure of the lens, which is also the obstacle to the extension of the schematic treatment to give a wide-angle schematic eye dealing with marginal rays and oblique incidence. YOUNG (1801) began the exploration of the peripheral image shell form in man, and several investigators have followed up his work. GULLSTRAND (1924) regarded the requisite information for this investigation as unavailable. The treatment of cornea form has been sophisticated in wide-angle schematic eyes (STINE, 1934; DRASDO and FOWLER, 1974) but relatively crude lens models are employed to consider obliquities of incidence up to 100° without verification from experimental measurement or from continuous media treatment of the lens.

The mathematical apparatus required for the general treatment of optic systems is provided by Hamiltonian optics (SYNGE, 1937; BUCHDAHL, 1970) which enables the whole system to be discussed in terms of its characteristic function. The difference between the characteristic function ideal for some specific purpose and its realisable form define the aberrations of the system. An early treatment of aberration in continuous nonhomogeneous media by BUCHDAHL has been extended by SANDS (see SANDS, 1973) to encompass media with discontinuities. SANDS's results have been put into a form suitable for computer analysis by MOORE (1971), and the implications of various radial and axial index gradients investigated. Current interest in such techniques is directed towards the exploitation of newly developing procedures for the production of inhomogeneous glass. The ability to treat inhomogeneous media, marginal rays, and oblique incidence make Hamiltonian optics a potentially powerful, although formidable, tool for the investigation of the isoindicial contours of the lenses of different species. MOORE (1971) has demonstrated that the axial gradient of index is similar in its influence to an aspheric surface, but that radial gradients enable the very ready control of the Seidel aberration coefficients. If the acceptable levels of peripheral aberrations differ in the effective image shells of frontal- and lateral-eyed species, then adaptations for their control might be revealed by comparison of the radial-index gradients.

4. Schematic Eye Parameters for Different Mammalian Species

GULLSTRAND's human schematic eye (1909) has not so far been replaced; for most purposes this would be unnecessary, because its dimensions and parameters are within 2% of the means for a population of 1000 eyes measured by STENSTRÖM in vivo (1946). Complete schematic eyes are now available for a variety of vertebrates, including the cat (VAKKUR and BISHOP, 1963; VAKKUR et al., 1963), rabbit (HUGHES, 1972), rat (HERMANN, 1958; BLOCK, 1969; HUGHES, 1977c), monkey (VAKKUR, 1967), gecko and iguana (CITRON and PINTO, 1973), pigeon (MARSHALL et al., 1973), frog (DU PONT and DE GROOT, 1976), and goldfish (CHARMAN and TUCKER, 1973); extensive measurements of the ocular dimensions of echolocating bats have also been provided by SUTHERS and WALLIS (1970). A detailed comparison of the results of these reports would be enervating, but in view of their value as a tool for comparative optical work, they have been summarised in Table 1.

These results are based upon measurements of populations of different size and techniques of varying reliability. The pooling of dimensions to give mean values before computation of the average eye also eliminates the influence of their covariation and will inevitably widen the confidence limits that can be put on the mean parameters for the whole eye. These effects are particularly important in small eyes and can make the schematic eye useless for the estimation of the mean refraction of the animal at the effective image plane (HUGHES, 1977c). It should be noted that the final refractive state of the eye is calculated from the difference between the length of the dioptric path to the plane of focus and the length of the eye to the effective image shell, i.e., from the out-of-focus distance. Certain authors have adjusted the calculated refraction by manipulation of the position of the effective image shell to match the retinoscopic refraction of the eye. In view of the results outlined in Section CIII, this practice (VAKKUR and BISHOP, 1963) is not advised, and the eye should, if adjusted, be brought to emmetropia. In other instances the schematic eye refraction is taken as that computed (HUGHES, 1972; HUGHES, 1977c) for comparison with the results of optometric refraction. A supplementary emmetropic eye is easily computed.

5. Comparative Ocular Structure

The system of equations which define the Gaussian schematic eye shows that neither its refractive state nor light-gathering efficiency are influenced by overall changes of size. W are led, therefore, to consider what factors may account for the 68-fold range of axial length to be found between the 0.8-mm-long eye of the shrew and the 54-mm eye of the baleen whale.

The size of the eye is related to that of the body according to HALLER (1769):

> Magnitudo ocularum est fere in ratione inversa animalium. Balaenae, Rhinoceroti, Elephanto parvi sunt oculi
> (The size of the eye varies inversely as the size of the body. The eyes are small in whales, rhinoceros and elephant)

Table 1

P = position R = radius relative lo corneal vertex (mm)	Man unaccom-modated		Man accom-modated		Monkey unaccom-modated		Monkey accom-modated	
	P	R	P	R	P	R	P	R
Anterior cornea	0.0	7.7	0.0	7.7	0.0	6.36	0.0	6.36
Posterior cornea	0.5	6.8	0.5	6.8	0.61	5.14	0.61	5.14
Anterior lenticular	3.6	10.0	3.2	5.33	2.25	?	1.75	3.58
Core anterior	4.146	7.911	3.873	2.655	—	—	—	—
Core posterior	6.565	−5.76	6.528	−2.655	—	—	—	—
Posterior lenticular	7.2	−6.0	7.2	−5.33	6.46	?	6.46	−4.55
Retinal surface	—	—	—	—	—	—	—	—
Inner limiting membrane	—	—	—	—	—	—	—	—
Choroid/retina	24.0	—	24.0	—	17.97	—	17.97	—
Posterior scleral	—	—	—	—	18.97	−11.0	18.97	−11.0
Cornea refractive index	1.376		1.376		1.376		1.376	
Aqueous refractive index	1.336		1.336		1.336		1.336	
Vitreous refractive index	1.336		1.336		1.336		1.336	
Lens capsule refractive index	1.386		1.386		—		—	
Lens core refractive index	1.406 eq.		1.406 eq.		—		—	
Effective index homogeneous lens	—		—		?		1.463	
Cornea, power Diopters	43.05		43.05		51.541		51.541	
Lens, power Diopters	19.11		33.06		38.168		60.109	
Eye, power Diopters	*58.64*		*70.57*		*82.916*		*102.807*	
Anterior Focal length; eye. mm	−17.055		−14.169		−12.0604		− 9.727	
Posterior focal length; eye. mm	22.785		18.930		16.113		12.995	
Anterior principal point; eye. mm	1.348		1.772		1.523		1.602	
Posterior principal point; eye. mm	1.602		2.086		1.857		2.013	
Anterior focal point; eye. mm	−15.707		−12.397		−10.538		− 8.125	
Post focal point; eye. mm	24.387		21.016		17.970		15.009	
Anterior nodal point; eye. mm	7.088		6.533		5.575		4.870	
Posterior nodal point; eye. mm	7.332		6.847		5.910		5.282	
Out of focus distance. mm	1.105		5.07		0.0		− 2.962	
Post nodal distance. mm	*17.055*		*14.169*		*12.061*		*12.689*	
Refractive state schematic. Diopters	1.0		− 9.6		0.0		−19.080	
Retinoscopic refractive state. Diopters	1.0		—		—		—	
Retinal magnification. mm/°	0.29 mm/°		—		0.25 mm/°		—	

Sources of data: man, HELMHOLTZ (1924); monkey, VAKKUR (1967); cat, VAKKUR and BISHOP (1963). HUGHES, (1976a); rabbit, HUGHES (1972); rat, HUGHES (1977c); goldfish, CHARMAN and TUCKER (1973); pigeon, MARSHALL et al. (1973); gecko and iguana, CITRON and PINTO (1973); frog, DU PONT and DE GROOT (1976). Refractive indices, FREYTAG (1910).

(FRANZ, 1934; WALLS, 1942; ROCHON-DUVIGNEAUD, 1943), but the eyes of these species are *large* in their absolute dimensions; the rule is obviously misstated and should refer to relative eye size. The universal application of the law is complicated by other generalizations, such as LEUCKART's law (1876) which states that swifter species have larger eyes.

The axial length of the eye varies almost linearly with the logarithm of body weight over a wide variety of species and great range of body weight. The allometrically more desirable plot of the logarithm of the axial length of the eye against the logarithm of body weight thus takes the form of Fig. 9A. At a given weight there is a three- to fourfold range of eye length, but this is reduced if the birds are treated as a separate distribution; in accordance with LEUCKART's law, their eyes are consistently larger than those of mammals of the same weight. It is

Cat		Rabbit		Rat		Bat	Pigeon		Frog		Goldfish		Gecko (Nocturnal)		Iguana (diurnal)	
P	R	P	R	P	R		P	R	P	R	P	R	P	R	P	R
0.0	8.57	0.0	7.5	0.0	2.965		0.0	3.44	0.0	3.08	0.0	3.0	0.0	4.48	0.0	2.6
0.68	7.89	0.4	7.1	0.26	2.705		—	—	0.15	2.93	0.036	2.964	0.44	4.48	0.15	2.6
5.2	7.2	3.3	6.9	0.881	2.34		1.77	4.17	1.7	2.9	2.036	1.1	1.7	3.26	1.07	4.83
—	—	—	—	1.778	0.958		—	—	—	—	—	—	—	—	—	—
—	—	—	—	3.695	0.958		—	—	—	—	—	—	—	—	—	—
13.7	− 8.05	11.2	5.8	4.591	2.34		4.7	3.08	5.91	2.5	4.236	1.1	7.4	3.05	4.22	2.17
—	—	—	—	5.981	—		11.27	—	—	—	5.446	—	—	—	—	—
—	—	—	—	—	—		—	—	7.7	4.28	5.546	—	11.0	—	8.7	—
21.83	—	17.9	—	6.154	—		11.62	8.41	—	—	—	—	—	—	—	—
22.3	−12.5	18.1	−9.8	6.292	3.23		—	—	8.0	4.6	4.2	—	—	6.5	—	4.9
1.376		1.376		1.38			—		1.39			—	1.36		1.35	
1.336		1.337		1.337			1.334		1.338			1.335	1.336		1.336	
1.336		1.337		1.337			1.341		1.338			1.337	1.336		1.336	
1.40		1.407		1.39			1.383		1.39			—	—		—	
1.448		1.457		1.5			1.409		1.47			—	—		—	
1.554		1.6		1.683			1.408		1.65			1.69	1.415		1.4	
											Water	Air				
38.914		44.6		112.649			—		109.1		0.8	129	—		—	
52.964		75.0		243.991			—		198.3		—	—	—		—	
77.983		*100.6*		*300.705*			*126*		*244.8*		*467*	*532*	*111.33*		*155.71*	
−12.823		−9.9		−3.326			−7.91		−4.08		−2.86	−1.88	−8.9		−6.45	
17.132		13.3		4.446			10.61		5.47		2.87	2.51	12.0		8.58	
4.514		4.0		1.651			0.76		2.32		1.39	0.92	1.44		1.87	
5.022		4.7		1.732			0.85		2.34		1.39	1.06	1.47		1.67	
−8.309		−5.9		−1.675			−7.15		−1.76		−1.46	−0.96	−7.5		−5.64	
22.153		18.0		6.178			11.46		—		4.26	3.57	3.6		10.3	
8.823		7.3		2.771			3.46		3.71		1.4	1.55	4.47		2.9	
9.330		8.0		2.852			3.55		3.73		1.4	1.69	4.51		3.79	
0.323		0.1		0.026			0.0		—		0.0	—	—		—	
12.5		*9.9*		*3.326*			*7.91*		*4.08*		*2.86*	*1.88*	*6.5*		*4.9*	
1.5		0.7		1.755			—		—		0.0	−130	—		—	
1.5		2.0		9.4			2.4		4.0		6.9	—	3.0		1.5	
0.21 mm/°		0.173 mm/°		0.06 mm/°			0.14 mm/°		0.08 mm/°		0.05 mm/°	—	0.11 mm/°		0.086 mm/°	

See SUTHERS and WALLIS (1970) for incomplete schematic data

clear from the graph that only the central region of the distribution approximates the slope of 0.3 which would be expected (GUNTHER 1975) for a linear dimension in such a plot; in small animals the eye length increases with body weight more rapidly than expected, and for the larger species its size is relatively independent of body weight. These results suggest that, given the nature of the elements common to its construction and the physical world to which it is adapted, a globe from 35 mm to 50 mm in diameter suffices to meet the most stringent requirements of species over a 10^4-fold range of body weight. This point was put by D'ARCY THOMPSON (1961):

> The eye, in short, can never be very small and need never be very big; it has its own conditions and limitations apart from the size of the animal. But the insect's eyes tell another story. If a fly had an eye like ours, the pupil would be so small that diffraction would render a clear image impossible. The only alternative is to unite a number of small and optically isolated simple eyes into a compound eye, and in the insect Nature adopts this alternative possibility.

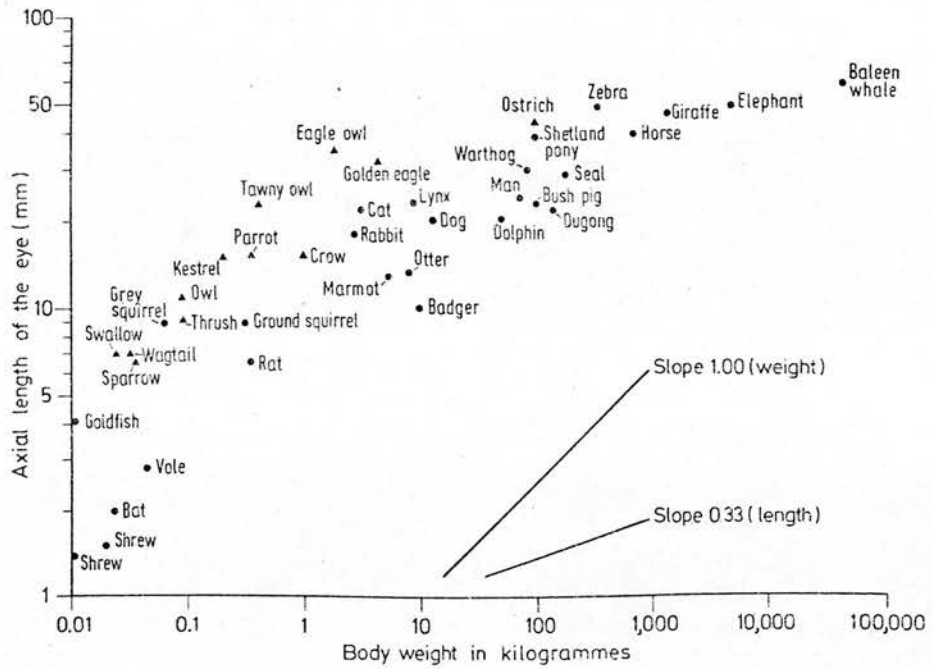
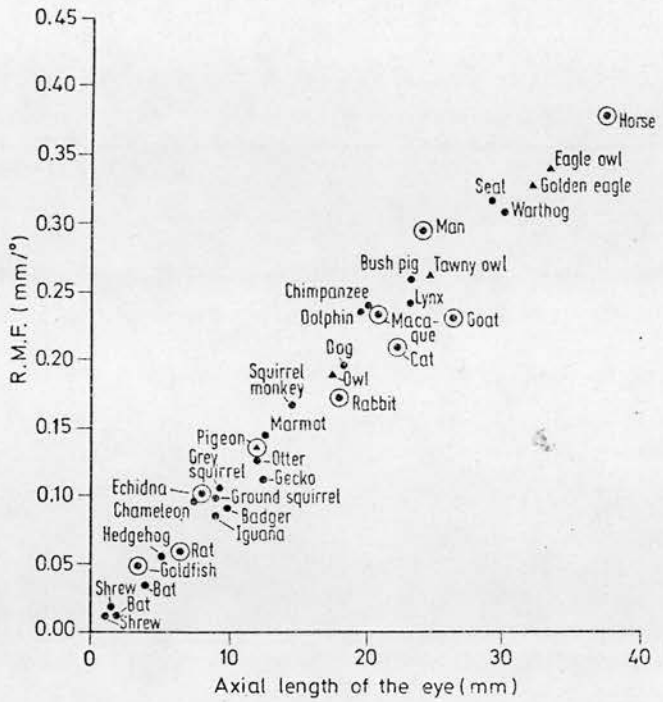


Fig. 9(a). Relationship between the axial length of the eye and body weight in birds *(triangles)* and other forms *(discs)*. Length of mammalian eye increases more rapidly with increase in weight than allometric proportion would suggest for the small species and more slowly for the large: in the intermediate range alone is the expected slope of 0.33 attained. An eye of 35–50 mm diameter meets the requirements of a variety of larger species over a 10^5-fold range of body weight. Sources various: schematic eyes if available, measurements from published photographs (e.g., ROCHON-DUVIGNEAUD, 1943), and unpublished data. Data has diverse origins but demonstrates a trend: too much reliance should not be put on individual points. (b). Retinal magnification factor (RMF) in mm/° as a function, of the axial length of the eye, *L*. The range of RMF at any given axial length is small considering the diverse sources of the data. The ratio of the posterior nodal distance (PND) to the axial length of the eye is thus relatively fixed and varies little between nocturnal and diurnal forms. The scatter diagram for this assortment of nocturnal and diurnal forms is well fitted by a regression line of slope of 0.011 mm/° per mm L and thus PND = 0.6 L. The RMF was derived from schematic eye data if available (circled points; birds triangles and others discs). In other instances the PND was estimated from the mean radius of curvature of the eye cup over an arc extending 45° each side of the optic axis in published photographs of eye cross sections

We have already seen that the refractive state of an eye remains constant with isomorphic scaling of the dioptric apparatus, however, the wave nature of light ensures that in an ideal optical system the highest spatial frequency, f, in the image shell is proportional to the pupil diameter, D, thus $f = D/\lambda$ (WESTHEIMER, 1972a). The illumination of a given area of image surface varies as the pupil area, D^2, and inversely as PND^2; illumination per unit retinal area thus remains constant with isomorphic scaling of an eye at a relative value indicated by $(D/PND)^2 = (1/F_{no})^2$. It was on the basis of this relationship that WALLS, (1942) wrote,

> an eye which is simply larger will not, then, have brighter images and greater overall sensitivity in dim light,'

but the last statement is not true. The absolute light gathering power of a scaled eye increases with pupil area, D^2, so that the *potential* absolute threshold



b

and increment sensitivity are improved because of the increased amount of light per unit solid angle of the image space (BARLOW, 1964); whether such potential is attained depends upon the strategy employed in sampling the image space. However, from the point of view of improving both resolution and absolute threshold it may be argued that nocturnal and diurnal species gain advantage from increased eye size which alone would not, therefore, enable the distinction of the two lifestyles. Whether or not a relatively large eye *is* developed depends upon the pressures encouraging reliance upon vision in a given species' niche; the eye of the mole (QUILLAM, 1966) is relatively small for an animal of its size.

Of course, the pupillary enlargement necessary to achieve an improved quantum capture and better resolution in the image plane need not be obtained by isomorphic scaling. An alterative is to increase the $F_{no.}$ of the eye by enlarging the pupil and thus transferring higher spatial frequencies to the brighter image plane. The quantum content per unit solid angle of the image space is the same for such an eye as for an isomorphically scaled eye of identical aperture and both forms require the same degree of pooling per unit solid angle in the photoreceptor system if the potential increase in sensitivity or absolute threshold is to be realised. However, to take advantage of the potential for increased resolution in the instance of increasing aperture alone it is necessary to reduce the sampling grain, assuming the original eye to be of optimal design, and this requires smaller photoreceptors. It turns out that the lower limit on eye size, in fact the whole design strategy for diffraction limited eyes organised for optimal resolution pivots around the minimum possible photoreceptor size. Isomorphic scaling is the optimal strategy for such eyes.

It has been demonstrated (SYNDER and MENZEL, 1975; PASK and SNYDER, 1975) that the angular acceptance of a photoreceptor, and thus its independence as a sampling element, is minimised when its waveguide parameter, V, has a value of about 2.5. Receptor diameter is then defined in terms of the wavelength of light, λ, and the difference between the refractive index of the receptors, n_1, and their surrounding medium, n_2,

$$d = V\lambda/\pi \sqrt{n_1^2 - n_2^2}.$$

The materials available in the eye set a minimum photoreceptor diameter of about 1–2 μ; if V were reduced to obtain a smaller photoreceptor then crosstalk with adjacent receptors would occur and the acceptance angle increase.

Now, we have that the highest spatial frequency in the image plane is $f \doteq D/\lambda$ cy./°; from sampling theory the minimum number of sampling elements per unit solid angle of retina which could resolve this frequency, f cy/°, is given by $(2f)^2$ and their angular separation, $\Delta\phi$, therefore by $\Delta\phi = 1/2f$; thus $\Delta\phi = \lambda/2D$ if they are arranged in a square matrix. The smallest possible eye capable of a given resolution with a square sampling array would have cones of the minimum diameter packed shoulder to shoulder and a PND sufficient to make the angle d/PND equal to the SHANNON-NYQUIST angular sampling rate $\Delta\phi = d/PND = 1/2f = \lambda/2D$ (KIRSCHFELD, 1976; SNYDER and MILLER, 1977). The optimal ratio of PND and D for a diffraction limited eye, $PND/D = 2d/\lambda = F_{no.}$ is thus defined and for typical values of $d = 2\mu$ and $\lambda = 0.5\mu$ would be $F_{no.} = 8$. SNYDER and MILLER (1977b) have derived from signal to noise considerations that the angular photoreceptor diameter, $\Delta\varrho$, which is optimal for a diffraction limited eye is given by $\Delta\varrho = 0.586\ \lambda/D$ which very closely approximates the maximum space available at the optimal sampling rate.

Would there be advantage in employing photoreceptors larger than the minimum possible size for an eye of optimal diffraction limited design? From above we see that for a given cut-off frequency, f, or pupil size, D, a larger photoreceptor of diameter, d, can only be accomodated by increase of PND and thus a decrease in the F_{no} and 'speed' of the eye. A further disadvantage of increase in PND whether under isomorphic of anisomorphic scaling results from a proportional increase in retinal noise if the tissues remain similar in properties (BARLOW, 1964). If the PND is alone increased then the eye is in this respect at an immediate disadvantage; by contrast, in isomorphic scaling the increased light capture and reduction in photon noise by the enlarged pupil would more than offset the increased retinal noise. The presence of retinal noise, however, reduces the expected reduction of absolute threshold and increment sensitivity upon isomorphic scaling of the eye (BARLOW, 1964). In real eyes, both uncorrected spherical and chromatic aberration also increase with the pupil diameter, although the latter varies inversely as PND so that isomorphic scaling leaves it unaltered. This suffices, however (BARLOW, 1964), to again reduce the improvement in image quality to be expected from an enlarged pupil, but the influence of aberration may be reduced by anisomorphic scaling. Quite apart from competition by other organs for space in the head, it is apparent that, for a diurnal diffraction limited eye with an adequate light supply, the minimum photoreceptor diameter and associated minimum PND have considerable inherent advantages, an increase in photoreceptor size would be positively disadvantageous. Whether a diffraction limited eye achieves its potential resolution is dependent upon the luminance level of the environment but SNYDER and MILLER (1977 b) point out that large and small eyes of optimal design, which are diffraction limited to high and low spatial frequencies respectively, achieve their maximum resolution at the same external luminance level.

Given such a theoretical background, the limited range of cone density encountered *in the areas of best vision* of vertebrates becomes comprehensible. Characteristic values would range between the 160000 cones/mm² in the human fovea (ÖSTERBERG, 1935) and the minimum densities of some 400000 cones/mm² encountered in the central areas of the hawk and eight other species of bird (FITE and ROSENFELD-WESSELS, 1975); early reports of foveal receptor densities in the order of 1000000 cones/mm² in eagle (POLYAK, 1957) and hawk (ROCHON-DUVIGNEAUD, 1919) have not been confirmed in recent studies. Away from the central area quite different considerations apply. Thus peripheral cones may be very large and have been argued to play a non-optimal resolution task as re-radiators of light to the rod system (MILLER and SNYDER, 1973).

Can these principles be discerned in the structure of real eyes? They are certainly helpful to qualitative understanding but in most species the eye is a compromise between conflicting requirements and a general analytic treatment of its design is not yet possible. Few species have a pure cone,

diffraction limited, central area in which photopic resolution is determined by the photoreceptor matrix; it is known amongst the homeotherms in primates and birds and may occur in some small, so-called, pure cone eyes such as those of tree shrew and ground squirrel. The high resolution of birds is legendary and is accompanied by the equally well known large eyes which would be expected from the above analysis. The pressure for high diffraction limited acuity in birds obviously leads to considerable difficulty in housing the necessarily large eyes; MILLER and SNYDER (1977) and SNYDER and MILLER (1977a) have suggested that the convexiclivate foveal pit of the bird is employed as the negative element of a telephoto lens system which, by magnifying the local image at the foveola, enables the eye to take advantage of an increased aperture to achieve resolution usually appropriate to a much longer eye.

As the environmental illumination is decreased, the diffraction limited eye suffers a reduction in its resolving power determined by the increasing photon noise; this may, over a limited range of intensity, be offset by increase in the pupil size until aberrations intervene to limit resolution once more. At the largest pupil diameter some further advantage may be gained by increased pooling in the sampling matrix. Under these conditions we are considering quantum, rather than diffraction, limited resolution so that design considerations change and are more difficult to discuss in detail.

The body of the globe may generally be approximated by a sphere and thus, if a limited area of the retina attains a diffraction limited sampling rate then its associated PND sets a radius, to a first approximation, for the remainder of the retina. Similarly, the evolutionary pressure on arhythmic and nocturnal forms to attain a low absolute threshold and high increment sensitivity may lead to a large diameter globe; one which is much larger than a diffraction limited globe would needs be in order to achieve the possibly modest photopic resolution of that species. On this basis it is perhaps comprehensible that eyes of quantum limited design may not possess regions for maximal photopic resolution which are of optimal diffraction limited design; the mere presence of both rods and cones in the central region of the area centralis of most mammalian species is sufficient to exclude optimal design. In the cat area centralis there are some 25000 cones/mm^2 and 360000 rods/mm^2 (STEINBERG et al., 1973). Under photopic conditions the pupil may be optimally adapted to the photopic receptor sampling density but the cone size and associated PND cannot be optimally matched. The maximum possible resolution of the cat cone population could be achieved by an eye of only one quarter of the size, but of course, such an eye would have a higher absolute threshold under conditions of low illumination. Eyes predominantly designed for crepuscular and nocturnal conditions would thus be expected to be larger than diffraction limited considerations would predict from their behavioural resolution. Clearly the whole strategy of eye design requires consideration of the relative importance of vision at different intensity levels with a resultant optimisation beyond the capacity of current models. No account has been taken here of the retinal reorganisation which occurs during dark adaptation (PIRENNE, 1962) or of the contending requirements of the peripheral retina for photopic and scotopic vision.

It does not follow, a priori, that the size of a diffraction limited eye should be calculable from its behavioural photopic resolution. Optimisation in the design is between the sampling matrix and image; only if there is 1:1 connectivity between the sampling elements and the brain: as in the human fovea, would behavioural resolution represent the potential of the sampling matrix. In the central area of most eyes, and the peripheral retina of all, the output of the photopic receptors converges onto ganglion cells with possible loss of independence and reduction of the behavioural resolution. However, the fine receptor matrix is employed in generating outer retinal subunits which are sensitive to movement thus justifying analysis in terms of diffraction limited organisation.

A similar argument has been put forward in relation to rod diameters. Central rod densities appear to cover a similar range to those of cones, with characteristic values of 400000 rods/mm^2 for rat (CONE, 1963) and about 400000 rods/mm^2 in cat (STEINBERG et al., 1973) in spite of a 3.5 fold difference in eye size. Anatomical convergence is so obvious in the first stages of rod connectivity that larger rods might be thought adequate. As RUSHTON (1962) asks,

'Would we not do just as well with giant rods a hundred times as big as they are?'

Although suggesting that speculation would outstrip propriety, he hazards that the answer might lie in the need for a fine scotopic grain for movement detection. The possibility that the rod matrix is employed in some form of discrete sampling is inherent in the recent observation of WEALE (1976) that the information content of the image plane is in reasonably close agreement with that attainable by sampling with the entire receptor matrix, not just the cone matrix, in both central and peripheral retina. Whether observations of the real optical system support this theoretical treatment remains to be seen.

Examination of Fig. 9A clearly shows that the dimensions of small mammalian eyes increase more rapidly in proportion to body weight than would be expected from allometric considerations; the requirements of these species thus seem to be constrained by the limited space available for housing the eyes in the head. In contrast, the larger animals have eyes of relatively uniform size over a considerable range of body weight which, unless there is some inherent limitation on, say, the size which a crystalline lens may achieve, indicates their needs to be met by, relatively, very small globes. Such a situation is very plausible. The need of large diffraction limited eyes for high resolution vision is predominantly centred on the detection and identification of either prey or predator at a distance adequate to respectively enable certain escape or stealthy approach. The inherent properties of an environment set limits on these requirements which are fairly independent of the size of its denizens e.g., distance vision is massively degraded by quantum limitations on moonless nights, no diurnal forest species can see further than the herbage density permits. Only a few environments, such as the open plain or that occupied by the raptorial birds, set a premium on high resolution vision. Thus the eagle, a relatively small animal, has perhaps the most acute vision of any species; its resolution would be quite unneccessary to the herbivorous elephant with its freedom from carnivorous predators. The possibility of very large quantum limited eyes arising in large animals which are active at very low light intensities seems to have been excluded by the development of alternate sensory systems; quantal limitations in such environments make adequate resolution impossible within a reasonable integration time.

These observations are clearly at variance with KIRSCHFELD'S (1976) concept of 'subjective resolution;' over a range of species from insects to mammals it is argued that resolution normalised to body height is constant within an order of magnitude. KIRSCHFELD suggests that small animals deal with the world at shorter distances and can thus resolve an object into the same number of points as does a larger from at a greater distance. There may be some truth in this hypothesis when applied to the whole gamut of species but within a group like the homeotherms it is a very crude approximation as indicated by comparison of the acuity of man and squirrel monkey (MERIGAN, 1976).

A given axial length may be achieved for an emmetropic eye by the choice of a great variety of corneal powers, lens powers, and separations of these components. Such differences are actually found to occur in the eyes of different species and may be attributed to specializations for nocturnal and diurnal vision. WALLS (1942) describes the lens of nocturnal species as relatively more powerful and situated further back than in a diurnal form of the same size. The more rearward situation of the posterior nodal point in such an eye results in a smaller PND and RMF (RMF = retinal magnification factor = $(PND\pi/180)$mm/°); the brightness of the retinal image is improved, because it varies inversely as the area of retina illuminated, i.e., proportional to $(1/PND)^2$ but at the expense of a smaller image. A plot of the RMF against the axial length of the eye shows the extent to which it varies with nocturnal and diurnal life styles at a given eye size. It is clear from the *estimated* RMF's plotted in Fig. 9B that the diurnal eyes tend to greater magnification than the nocturnal, but the range is limited and rarely exceeds 20% of the mean value. The trend to strong proportionality between RMF, or PND, and

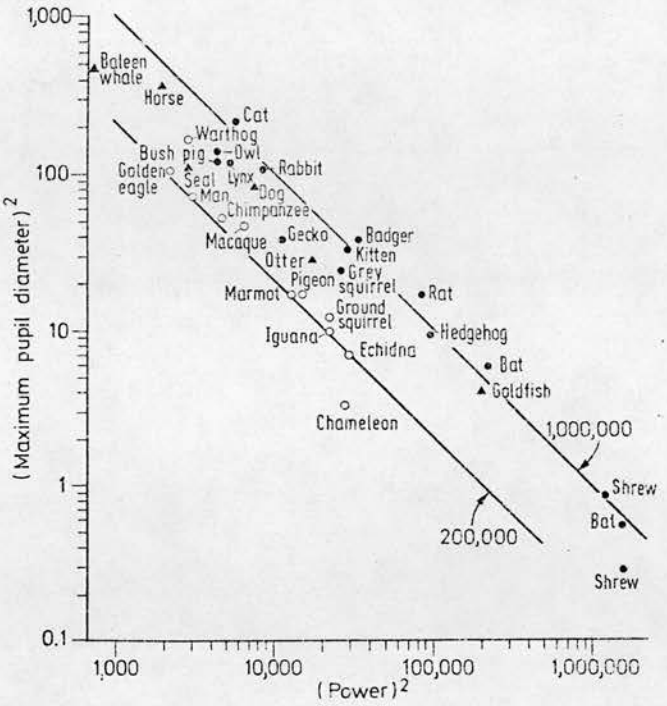


Fig. 10. Light-collection factor: square of maximum entrance pupil diameter, D_m (estimated as 90% of lens equatorial diameter in mm corrected for corneal magnification if not known from direct measurement) plotted against retinal distance factor, the square of the power of the whole optic system of the eye, estimated as $(1/\mathrm{PND})^2$ determined from the radius of curvature of the eye cup, in meters, if not available from a schematic eye. Animals whose points fall on a given isoillumination line have the same retinal illumination under given conditions of ambient lighting when the pupil is fully dilated. Of the available species it is obvious that the nocturnal forms lie close to the 10^6 illumination line, for which the f No. is given by $\mathrm{PND}/D_m = 0.95$, and the diurnal forms lie close to the 2×10^5 line corresponding to an f No. of 2.1. The range of maximum f Nos. is thus small for a wide variety of forms and the diurnal and nocturnal animals differ only fivefold at most, in their retinal illumination with fully dilated pupils. From the legend of Fig. 9 B we may conclude for extreme nocturnal forms that $D_m = 0.63L$ and for extreme diurnal species that $D_m = 0.29L$. Note that kitten, cat, and rat have similar light collecting power in spite of the difference in size of their eyes

axial length is apparent, but quite small variations in PND have a significant influence on the retinal image brightness because of the inverse square relationship between the two factors.

The amount of light which enters the eye is determined by the area of the entrance pupil; for a given axial length its maximal value shows a good correlation with nocturnal and diurnal habits. A useful index of the light-gathering power of the eye may thus be obtained as $p^2/(\mathrm{PND})^2 = (1/\mathrm{F}_{NO}^2)$, where p is the maximal entrance pupil diameter and units arbitrary. Sufficient complete schematic eyes are not available for an informative graph to be made from their parameters, but the necessary measurements may be approximated as described in the legend of Figure 10, in which a function of the maximum entrance pupil area has been plotted against the image area factor.

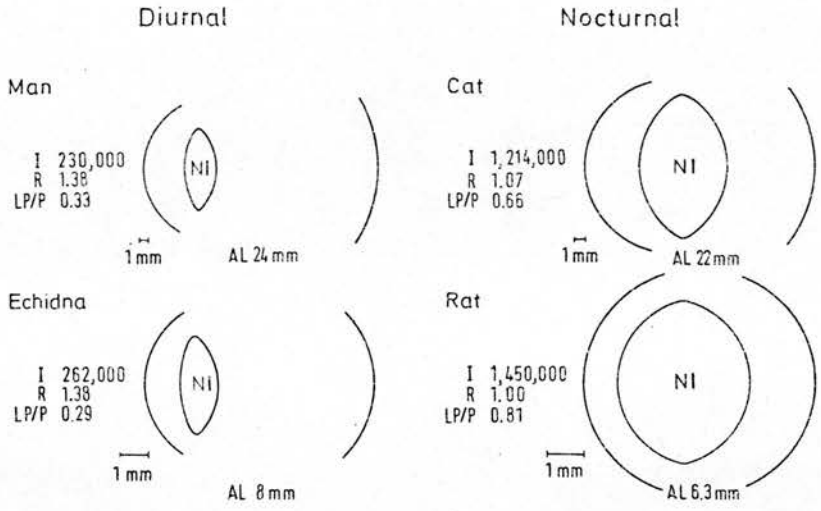


Fig. 11. Human, echidna, cat, and rat eyes scaled to the axial length of the rat eye. Optic design is obviously related to the nocturnal/diurnal division rather than to absolute size. Retinal illumination index, I = pupil area/(posterior nodal distance)^2, is independent of scaling and clearly differentiates diurnal man and echidna from nocturnal cat, and rat. As discussed in text, the retinal image in the scaled diurnal eyes is about one-third larger than in nocturnal forms (R = scaled image size for animal/scaled image size for rat) thus enabling increased resolution with loss of brightness. Smaller, brighter image of the scaled nocturnal eyes is achieved, because the ratio of lens power to total power of eye, LP/P, is greater than in the diurnal species

Species located on the same $-45°$ isoillumination line in Figure 10 will have retinal images of the same illumination when their pupils are fully dilated under common conditions of illumination. It is striking to note the manner in which the indices for the eyes of obviously nocturnal species fall on, or close to, the 10^6 illumination index line. The cat and, potentially, the 1-day kitten eyes are thus of similar light-gathering power to those of the rat. From a given nocturnal eye, such as that of the rabbit, we may pass on the graph to a diurnal eye of either similar PND but smaller maximal entrance pupil, e.g., gecko, or to one of larger PND and similar maximal entrance pupil, e.g., eagle. The range in $(1/\mathrm{PND})^2$ at a given pupil size between nocturnal and diurnal species is somewhat less than 1 log unit, and a similar range of pupil area is found at a given PND. The illumination index thus differs fivefold between truly diurnal species, such as the marmot, and nocturnal types, such as the hedgehog and rat. Among the smaller eyes it is the reduced PND and RMF which predominate in establishing the retinal illumination. Among the larger it is the relatively increased pupil area which plays the major part.

Schematic cross sections of the eyes of man, echidna, and cat have been normalized to the rat eye on the basis of axial length (Fig. 11) in order to illustrate the influence of the factors discussed in this section on optic organisation. Various parameter values for each eye in its original and scaled-down form accompany the figures.

The cat and rat are arrhythmic species primarily adapted to nocturnal conditions but evincing diurnal activity. The eyes of man and echidna represent those of typical diurnal adaptation, although the two species are again flexible in behavior. Although reportedly a nocturnal animal, the echidna in fact spends a great deal of its time abroad during the day (COLEMAN, 1934, 1935) and has been found to possess cones (unpublished observations) and is thus not a pure-rod retina as previously described (O'DAY, 1939; WALLS, 1942). The fivefold greater illumination index of cat and rat over the human and echidna eyes reflects these differences in behavior. It should be noted that the relative proportions of the index attributable to the PND and pupil area change with scaling of the eye, but the overall index remains independent of size for a given optic organisation. The position of the lens and its power in relation to that of the cornea and maximum pupil diameter are very similar in the normalized sections of each nocturnal and diurnal pair in spite of the 300% difference in the absolute size of their globes.

The more posterior position of the lens in the scaled nocturnal relative to the diurnal eye has been shown to increase the image brightness. The consequent increased separation of the lens from the cornea necessitates a greater lens power in order to maintain that of the eye, and an additional increment of power is also required to return the eye to emmetropia. To effect this, it is necessary that the lens increase in surface curvature; this must be accompanied by an increase in thickness if the equatorial diameter and effective pupil aperture are to be maintained; a further increase in lens thickness is necessary if the eye is to obtain a larger pupil. The rearward displacement of the lens facilitates the housing of its greater equatorial diameter. The corneal base may also be relatively enlarged in order to enable the larger pupil aperture to be employed, but its extent does not play an important part in defining the total field of the eye.

The optic organisation of cat and rat, in spite of almost identical retinal illumination indices and total normalized power, differ much more than that of the human and echidna. The equatorial plane of the rat lens is situated in a similar relative position to that of the cat, but the lens itself is relatively thicker and more powerful. Because of the similarity of total normalized power and refractive state in the eyes of these two species, it follows that the rat cornea must provide a smaller proportion of the total power than does that of the cat, some 43% compared with 55%. The consequent relatively reduced curvature of the rat cornea is accompanied by an increased height which exposes more of the peripheral lens to oblique rays than in the cat eye. No obvious explanation of this is available in terms of the previous discussion, but it may be pertinent that the rat visual axis is some 60° anterior to its optic axis; an increase in the effective entrance pupil for oblique rays when the pupil is fully dilated could be of great benefit for forward vision.

II. Nonaxial Optics

1. Marginal Rays

a) Spherical Aberration

Marginal rays incident upon a spherical refracting surface are brought to a nearer focus than paraxial rays—spherical undercorrection. This *spherical aberration* may be calculated for the human (LE GRAND, 1942) or animal cornea upon the assumption that its surface *is* spherical in form, but, in fact, it is elliptical in man and flattens perceptibly towards the periphery (DUKE-ELDER, 1958; HAGE and BERNY, 1973). Such flattening is characteristic of an *aplanantic* surface in which the peripheral power is lowered to eliminate or minimise spherical aberration. The positive aberration of the human cornea may have been reduced by peripheral flattening but is not eliminated and is especially prominent in the aphakic eye when the pupillary diameter reaches 6 mm with the result that scotopic vision is poor (HAGE and BERNY, 1973). Peripheral flattening of the cat cornea has been reported (VAKKUR et al., 1963) and is apparent in the rabbit (HUGHES, 1972). The rat cornea is spherical (HUGHES, 1977c).

A homogeneous lens of conventional schematic eyes also demonstrates strong spherical undercorrection. By contrast, the actual crystalline lenses of cat (VAKKUR and BISHOP, 1963) and rat (HUGHES, 1977c) are found to display negative spherical aberration in the "cone of confusion" of their emergent ray bundles. A detailed analysis of the refractive-index gradient in the rabbit crystalline lens has shown it to offset the spherical surface-induced undercorrection to the extent that the system is overcorrected; marginal rays are thus brought to a focus further away than the paraxial rays.

The negative aberration of the lens may obviously play a part in offsetting the effects of the positive spherical aberration of the cornea. In spite of corneal aberration, at pupil diameters of less than 2 mm the human eye is almost free of overall aberration (HAGE and BERNY, 1973). Most commonly, the positive aberration of the cornea predominates (STINE, 1930) up to a maximum of some 7 D extra power, which makes the refraction myopic through the pupil periphery. Considerable variation of power occurs from one quadrant of the pupil to another (VAN DEN BRINK, 1962), and its pattern may change during accommodation.

The spherical cornea and homogeneous lens of the GULLSTRAND (1924) schematic eye lead to pronounced undercorrection along the optic axis; the introduction of an accurately aspheric cornea halves this aberration (LOTMAR, 1971). In the real eye, the remaining aberration is offset by the lens. The negative aberration of the lens has been simulated in recent extensions of the Gullstrand schematic eye either by the introduction of an arbitrary aspheric rear surface or, more satisfactorily, by the use of an approximate seven-shell model (LOTMAR, 1971). An accurate model lens has not been so far employed in a human schematic eye, although the extent of the crystalline lens axial aberration has been computed from the refractive-index gradient of five human lenses by NAKAO et al. (1969).

Little information is available about the spherical aberrations of lens and eye in species other than man. The obvious negative aberration of the cat and rat lens show that compensation for corneal undercorrection would be possible as in man. The overall aberration of the cat eye is not known, but its analysis in the rat (HUGHES, 1977b) provides an interesting contrast to man. The optometric refraction of the rat eye through the peripheral pupil by means of marginal rays indicated some 8 D greater hypermetropia than for central axial rays. It was also found that neurophysiologic refraction indicates as much as 10 D of hypermetropia when the pupil is dilated, although the eye appears to be emmetropic when the pupil is constricted (HUGHES, 1977b). It is interesting to note that the overall aberration of the rat eye is negative, like that of the lens, but that in man it is usually positive, like of the cornea. Examination of Figure 11 reveals that the rat lens takes precedence over the cornea in determining the power of the eye, whereas for the human the reverse is true. These gross aberrations predominate in the rat, as in man, at pupil diameters such as would be encountered only under scotopic conditions when quantum limitations restrict their influence on resolution.

b) Entrance and Exit Pupils

The need to consider marginal rays arises when dealing with pupillary optics. The entrance pupil of the eye is the image of the real pupil formed by the cornea

and determines the quantity of light which enters the eye. Calculation of its diameter when small is relatively straightforward (BENNETT and FRANCIS, 1962), but ray tracing, either calculated or geometric, is strictly required to specify its parameters when large. By this means both marginal rays and deviation of the cornea from sphericity may be taken into account. The average *calculated* entrance pupil diameter for an 80% dilated real pupil in the cat (VAKKUR and BISHOP, 1963) was, however, only 3% larger than the measured entrance pupil when derived according to Gaussian theory.

For the geometric specification of blur-circle diameters in the defocused eye, it is necessary to compute the size and position of the *exit pupil*, which is the image of the real pupil in the crystalline lens. Invariably only approximations of these parameters are obtained. If the homogeneous lens model is regarded as acceptable, it is possible to determine the exit pupil size and position for a small real pupil either by vergence calculation according to the Gaussian approximation or by ray tracing, but only the latter method may be used for larger pupils which accept marginal rays. The significance of such calculations is debatable, because they should be performed for a non-homogeneous thin-shell lens. No experimental determinations appear to have been made of the exit-pupil dimensions in the mammalian eye, so the error inherent in the common approximate computations is not known. For critical work the exit-pupil positions and sizes reported for the cat (VAKKUR and BISHOP, 1963) and rat (HUGHES, 1977c) should be regarded with scepticism until confirmed experimentally.

2. Oblique Rays

a) Oblique Axial Aberrations

The difficulties entailed in tracing rays which enter the eye oblique to the optic axis have already been attributed to the gradient of refractive index through the lens. YOUNG (1801) computed oblique-ray image shells for the human eye on the assumption of a homogeneous lens, and since that time there has been little improvement in the methods employed. The intrinsic complications of the subject are great; the shell of focus for horizontal and vertical sections through an oblique ray bundle differ in position, the oblique astigmatic difference or STURM'S interval, by an amount varying in man between 2 and 10 D at 60° eccentricity. In some people the retina lies between these two shells, in others to one side (FERREE and RAND, 1932). Other aberrations such as coma are potentially significant but may be minimized by the refractive-index gradient of the lens (NAKAO et al., 1968) so that their consideration requires a schematic eye with at least a thin-shell lens model. The PND of the optic system decreases for rays of increasing obliquity, and thus the overall refractive error of the eye depends upon the extent to which the retinal shell is deformed from a sphere to accommodate this. The retinal magnification factor may thus decline in the periphery, but its magnitude is determined not only by the PND but also by the angle subtended between the local retinal surface and the eccentric chief rays. A full treatment of peripheral imagery has not been attempted for any species. Some wide-angle schematic eyes have been developed for man (LOTMAR, 1971; DRASDO and FOWLER, 1974) but are

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Table 2

	Horizontal field			Vertical field
	Calculated		Measured	Measured
	Minimum	Maximum		
	/°	/°	/°	/°
Cat	158	214	181	180
Rabbit	168	212	192	180
Rat	147	238	205	198
Goat	—	—	190	186
Horse	—	—	193	178

Sources of data: cat, VAKKUR and BISHOP (1963), HUGHES (1976a); rabbit, HUGHES (1972); rat, HUGHES, (1977c); goat, HUGHES and WHITTERIDGE (1973); horse, HUGHES (unpublished observations).

based on homogeneous lenses and must therefore be accepted with caution: agreement between their performance and that of the eye may have been obtained simply by arbitrary modification of their parameters.

b) Uniocular Optical Field of the Eye

A primary application of wide-angle human schematic eyes has been the investigation of the nonlinear projection of the visual field onto the retina. The peripheral retinal magnification factor is said to be halved relative to its central value in man (DRASDO and FOWLER, 1974). The computed intraocular angle subtended between an image and the optic axis was some 90% of that subtended by the object over most of the uniocular field, although in the extreme periphery this value dropped to 70%. In the cat (HUGHES, 1976a) the measured variation of RMF was found to be much smaller and the retinal image to be a rather better central projection than calculated for man.

The theoretical extent of the uniocular field of an eye unobstructed by the ocular adnexa should strictly be assessed by means of a schematic eye equipped with a nonhomogeneous lens. For some purposes this may be avoided by employing the observation that a ray which subtends a straight line of the equatorial margin of the opposite side of the lens, when refracted by the cornea, will pass into the vitreous humour, while one which grazes the lens vertex will not (VAKKUR and BISHOP, 1963). Back tracing of these rays sets an upper and lower limit on the extent of the visual field in the plane considered. Such limited tracing has been made for several species of mammal, the results of which are included in Table 2. It is to be emphasised that, contrary to frequently encountered statements in the literature (DUKE-ELDER, 1958), the extent of the cornea does not necessarily determine that of the optic field of view; the relative position of the lens and cornea is more important.

Criticism has already been made of the methods commonly employed for the determination of the extent of the uniocular optical field. Thus the transcleral illumination technique reveals the cat optic field to be 150° (VAKKUR and BISHOP, 1963), whereas the use of perimetric ophthalmoscopy indicates 181° (HUGHES,

1976a). In contrast to the transcleral technique, in which the dense pigment and thickening at the ciliary body may restrict observation of the image, the results obtained by ophthalmoscopy usually agree substantially with the mean of the calculated limits; rabbit (HUGHES, 1972), cat (HUGHES, 1976a), rat (HUGHES, 1977c), goat (HUGHES and WHITTERIDGE, 1973). The range of horizontal uniocular optical field is from about 180° in cat (HUGHES, 1976a) to 205°–207° in rat (LASHLEY, 1932; HUGHES, 1977c); a horse eye with dilated pupil was found to possess a horizontal field of only 193° (HUGHES, unpublished observations) in contrast to the 215°–228° commonly attributed. The vertical field is much more uniform between species and extends for about 180°.

The elongated pupillary aperture of the horse, goat, and other ungulates has been suggested to extend the uniocular field, but the validity of this assumption remains untested. It doubtlessly does increase the effective entrance pupil for oblique rays passing to the forward fixation area.

III. Refractive State of the Vertebrate Eye

1. Axial Refraction

a) The Retinoscopic Refractive State

Modern visual dioptrics began with KEPLER's (1604) hypothesis that the vertebrate eye is effectively a *camera obscura* in which the objects of the external world are imaged upon the superficial retina by means of the spherical refracting surfaces of cornea and lens. SCHEINER (1619) was able to confirm this theory to the extent of demonstrating the presence of an image in the retina, but it remained for MÜLLER (1853) to conclude that the visual process is initiated, not on the vitread retinal surface, but at specialized photoreceptors in the sclerad border.

We have previously seen how the extent of the retina, the uniocular field, and the relative position of the two eyes determine the angular extent of the external object space encompassed by the visual field. It is characteristic of an optic system of power, D, however, that image quality is optimal in terms of resolution and contrast at only one distance, v, which is conjugate with a unique object distance, u, so that for a simple thin lens,

$$v = \frac{1}{1/u + D}$$

The photoreceptors define the effective image plane of the eye, and the conjugate object plane is thus established by the power of the optic system, D. Many species employ an accommodatory mechanism to vary their optic power and thus obtain good imagery over a wider range of object distance. In spite of this dynamic range of accommodation, only two static refractive states are commonly considered, the anatomic and the physiologic conditions of rest. The former is established with the lens in its state of maximum flatness and accommodation relaxed, either voluntarily or by means of drugs, while the latter incorporates some degree of accommodatory tone under defined field conditions. If parallel light from distant objects is brought to a focus in the photoreceptor plane then, for rough ophthal-

mologic purposes, the eye is described as emmetropic, and the optimal images of nearer objects may be displaced from the photoreceptor plane—although other factors may permit some depth of field to exist. There is no a priori reason to expect the anatomical or physiologic resting refractive condition to be emmetropic in all species; it is arguable that animals dealing with close objects (WALLS, 1942) might find a myopic refraction, perhaps focussed at the hyperfocal distance, more suited to their requirements. More extreme myopia, or even hypermetropia, need not be disadvantageous if the accommodatory mechanism is such as to permit reflex emmetropia.

The objective assessment of the refractive state of an eye is almost invariably attempted with retinoscopy. By this means the vergence of the emergent rays of the fundus reflex is measured and the extent of the separation of their surface of origin from the posterior focus of the eye thus established. If the emergent rays are parallel, then the principle of optic-path reversibility establishes that incoming rays from distant objects will be brought to a focus in the plane of origin of the fundus reflex; this condition is commonly described as emmetropic upon the implicit assumption that the reflex originates at the photoreceptor plane. There is no evidence that is does; such "objectively" measured emmetropia may represent subjective ametropia; however, the majority of the literature is based upon this procedure. The classic *conception* of the static mammalian refractive state with relaxed accommodation (e.g., LANG and BARRETT, 1887) is well summarized by JOHNSON (1901) on the basis of his ophthalmoscopic and retinoscopic observations of 182 species:

> A slight degree of hypermetropia, i.e. under 1 Diopter, may be said to be the rule throughout the higher Mammalia, whilst higher hypermetropia, i.e. 2 D to 5 D, is found in the wild species of the Rodents, the Edentata, and the Marsupials. *Simple emmetropia is rarely met with; indeed I very much doubt whether it is compatible with sight of a high degree of perfection.* From examination of the vision among a large number of native youths from the Upper and Lower Congo, the Nile Valley, and the Niger Territory, I found that every one with vision beyond the standard of 6/6 or 6/5 was hypermetropic to at least 0.5 to 0.75 Diopter (manifest), an amount closely corresponding with that found in the great majority of Primates and Carnivores.

Not all authors have obtained results in agreement with JOHNSON (1901). For instance, the rat eye has been described as from −13 D to −3 D myopic [scleral image focusing (LASHLEY, 1932); retinoscopy, vessel ophthalmoscopy, single-unit receptive field size (BROWN and ROJAS, 1965); retinoscopy (MONTERO et al., 1968)] as well as from 9 D to 20 D hypermetropic [retinoscopy (GLICKSTEIN and MILLODOT, 1970); retinoscopy (HUGHES, 1977a); retinoscopy (BLOCK, 1969)]. Again, dogs have been described as considerably myopic (UBERREITER, 1959), slightly myopic (WORFOLD, 1965), emmetropic (VOGT, 1936), or occasionally as hypermetropic (SMYTHE, 1961).

It is curious that the rhinoceros is so consistently described as myopic that such ametropia is sine qua non for the animal even in children's literature (Fig. 12). This prejudice—because it is apparently not based upon refraction—appears to have been well established by 1801 (LEIGH THOMAS, 1801), but to date no additional information about the rhinoceros eye is available which might engender doubt about Thomas's conclusion that,

> 'if we should ever become aquainted with the natural habits of this animal, his vision will be found to be as perfect as that of any other of the same class.'

Fig. 12. Acceptance of nonemmetropic refractive states in the animal eye is so prevalent that even the children's literature describes the rhinoceros as short-sighted! (After "Rupert the Rhinoceros" Little Golden Books, USA)

Such variability of results is understandable but necessitates careful consideration of published animal refractions. Ophthalmoscopy is not an acceptably accurate technique for refraction, and retinoscopy requires a modicum of skill. The state of accommodation of the animal or observer is rarely monitored during either procedure, and retinoscopy eliminates only the influence of the observer if a cycloplegic is not employed. Mydriasis concurrent with cycloplegic retinoscopy may, however, introduce peripheral aberrations so that the refraction does not represent the state of the eye when the pupil is small under normal photopic conditions. Additional discrepancies will arise if the results do not refer to a common spectacle lens plane.

It is essential that studies of the refractive state in a given species be based upon a reasonably large sample in order to allow for a range of ametropia within the population. The distribution of refractive error in large populations has only been established for macaque, chimpanzee (YOUNG, 1963; YOUNG and FARRER, 1964), and man (see DUKE-ELDER, 1970). In man the distribution is not normal (STROMBERG, 1936).

The great excess of human hypermetropes of low degree over the statistical expectation suggests covariation between the various optic components of the eye during growth to produce a much smaller spread of refractive error than would occur if their values were uncorrelated; these compensatory processes have also been demonstrated in the rabbit (LUDLAM and TWAROWSKI, 1973). There is no information about the population distribution of refractive errors or refraction during growth in other species, and it cannot be said whether "emmetropization" is universal. If the small population refractions available for other mammals are assumed to be normal distributions, then their standard deviations are very simi-

lar for a variety of eye sizes and range from 1 D to 2 D (Fig. 13), as in the human population.

JOHNSON (1901) considers myopic refraction common only in domestic animals, such as horses (LANG and BARRETT, 1887), cattle (DUBAR and THIEULIN, 1927), and especially hutched animals. Support for the long-debated influence of the visual environment on the refractive state of the eye is available from studies on monkeys (YOUNG, 1961, 1963; YOUNG and LEARY, 1973) and cats (ROSE et al., 1974). Street cats were found to show a mean refraction of 1.15 D $\pm$ 0.18 D whereas caged animals were overtly myopic at -0.62 ± 0.24 D with insignificant difference of mean axial length between the groups.

The 3 D myopic refraction of the rat eye (LASHLEY, 1932) and -15 D for teleosts (FRANZ, 1931) were accepted by both WALLS (1942) and DUKE-ELDER (1958), although conflicting results were available, as adaptations for near viewing. More recently, however, both rat (BLOCK, 1969; HUGHES, 1977b) and the teleosts (BARON and VERRIER, 1951; BAYLOR and SHAW, 1962; CHARMAN and TUCKER, 1973) have been shown to be of hypermetropic refraction. The consensus of modern workers is in agreement with the view of JOHNSON (1901) that mean retinoscopic hypermetropia is universal among wild mammalian species, which is puzzling; emmetropia or myopia is teleologically more comprehensible.

b) The Effective Image Shell

It is to be emphasized that retinoscopy simply indicates the separation of the reflective layer from the posterior focal plane of the eye and does not specifically determine the refraction of the photoreceptor plane. The surprising universal mean hypermetropia revealed by retinoscopy may thus be of little relevance in the consideration of subjective or behavioral refraction at the photoreceptor plane.

It is important for the ensuing discussion to identify the exact position along the photoreceptor at which light is brought to a focus during normal vision. Light has commonly been regarded as equally effective if in focus at any point along the axis of the photoreceptor outer segments. WALLS (1942) thus suggested that the elongation of the outer segment might be employed in certain species to minimize accommodation by the production of a greater tolerance for the plane of focus. The more recent concept of the photoreceptor as a waveguide (ENOCH, 1961) and/or "funneling" device (RUSHTON, 1956, 1963; DONNER and REUTER, 1965) implicates the inner segments of both rods and cones (BRINDLEY, 1966) as collectors of light for the outer segment, the basal diameter of the inner segment determining the receptor's entrance aperture (SNYDER and MENZEL, 1975). Under these conditions the directional properties of the receptors (STILES and CRAWFORD, 1933; BAYLOR and FETTIPLACE, 1975) require that the receptor axis project to the center of the exit pupil of the eye for optimal light capture. The placement of the exit pupil forward of the centre of curvature of the retina thus ensures that the more peripheral receptors would be set at an angle to the radial axis of the retina. Such oblique orientation of the peripheral receptors has indeed been reported in monkey, rabbit (ENOCH, 1972), fish, frog, and gecko (LATIES and ENOCH, 1971) as well as psychophysically demonstrated in man (ENOCH and HOPE, 1972). In all of these species the receptor orientates about the *beginning* of the inner segment, not about

the junction of the inner and outer segments, in a manner consistent with its presumed role as the entrance aperture. Optimal resolution would thus be achieved when the circles of least confusion of an image for which the eye is focused are coplanar with the receptor entrance apertures; these are aligned in the eye along the outer limiting membrane. The outer limiting membrane may therefore be taken to represent the presumed effective posterior focus of the eye and defines a shell in the light flux through the eye which is subsequently referred to as the *effective image shell*. It is to this shell that light will be brought to a focus during accommodation and subjective refraction.

c) Glickstein and Millodot's Explanation of Mean Retinoscopic Hypermetropia

In 1894 BEER noted that the true refraction of the photoreceptor surface is not obtained by focussing on the retinal blood vessels during *ophthalmoscopy*. In man the separation of the effective image shell from the vessels is necessarily small, relative to the posterior focal distance of the eye. The error in assessing the refractive error introduced by the separation of the plane of reflection from the effective image shell would thus make a subjectively emmetropic eye appear spuriously myopic if the plane of reflection lay behind the receptors and hypermetropic if in front. The almost universal mean hypermetropia described by JOHNSON (1901) and KAHMANN (1930) thus suggests a common reflecting surface forward of the receptors in the majority of species. GLICKSTEIN and MILLODOT (1970) found the magnitude of the retinoscopic error to be inversely proportional to the square of the posterior focal length of the eye, thus explaining WALLS' (1942) observation that

> As the size of the eye diminishes from that of a cat to that of a mouse... an increase of the hypermetropia from half a diopter or so to five, seven or even ten diopters (occurs).

Such an explanation would also account for the reduction of the mean hypermetropia of 2–3 D in human infants (GRAHAM and GRAY, 1963; SEBA, 1974) to some 0.5 D in the adult population as the eye grows from 17.9 ± 0.1 mm (SORSBY et al., 1961) to 24.0 ± 0.03 mm (STENSTRÖM, 1948). A similar change occurs in the refractive state of the growing rabbit eye (LUDLAM and TWAROWSKI, 1973) and during the growth of the eel eye just before breeding (WALLS, 1942).

Recent, careful retinoscopic investigations of a wide variety of species have been combined in Figure 13, with those of GLICKSTEIN and MILLODOT (1970) to display the relationship between the refractive state and axial length of the eye. These data are well fitted by a curve derived from the theoretical equation relating axial length and refractive state. The plane of reflection was estimated by GLICKSTEIN and MILLODOT (1970) to be displaced on average by 135 μm vitread of the posterior focus of the eye, a position which is consistent with reflection from the boundary between the vitreous and retina in the functionally emmetropic globe. It was thus concluded that *the almost universal hypermetropia established by retinoscopy results from a systematic error of method, and that the true mean refractive state of most, if not all, wild vertebrate species is close to emmetropia in the effective image plane.*

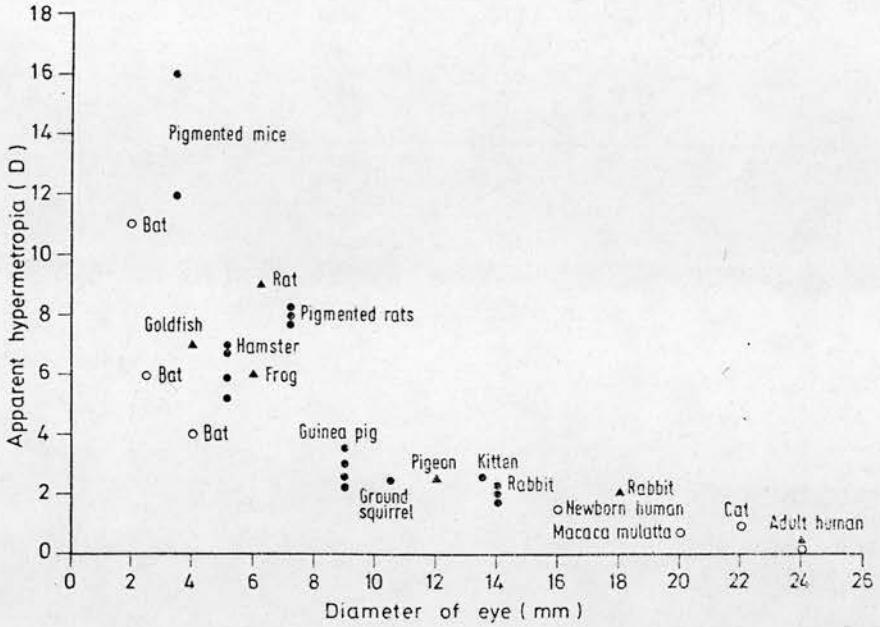

Fig. 13. Retinoscopic refraction as a function of the axial length of the eye. The graph well illustrates the marked hypermetropia of small eyes. (After GLICKSTEIN and MILLODOT, 1970, with a few additions)

These results clearly suggest the abandonment of WALLS' (1942) view that their hypermetropia shows

> the indifference of mice and mouse sized mammals in general to any refinements of vision relating to resolving power

and that

> many mud-grubbing, small eyed fishes are hypermetropic, indicating a loss of importance of vision to them.

d) Experimental Evidence for Glickstein and Millodot's Theory

The hypothesis of GLICKSTEIN and MILLODOT (1970) accounts well for the relationship between eye size and apparent retinoscopic hypermetropia but still requires proof by the demonstration that mean retinoscopic hypermetropia is accompanied by mean emmetropia at the effective image shell, and that the predominant fundus reflex arises at the border between the retina and vitreous humor. In keeping with the hypothesis, it is well known that a mean hypermetropia of about 0.5 D is detected in humans by retinoscopy when the eye is subjectively emmetropic (BALDWIN, 1964; FRY, 1967; SOUTHALL, 1926).

Evidence for the emmetropic state of the effective image shell is rare in other species of mammals which evince overt retinoscopic hypermetropia. Reports of the retinoscopic refraction of the cat indicate a mean hypermetropia from +0.8 D to 1.5 D (HESS and HEINE, 1898; VAKKUR et al., 1963; ROSE et al., 1974). The

refractive state at the effective image shell of the cat eye is in principle readily determined by electrophysiologic refraction during which the receptive field map or, for certain classes of retinal single unit, the response to light spots (HILL and IKEDA, 1971; IKEDA and WRIGHT, 1972) and to grating patterns (BARLOW and LEVICK, 1965) are used as a direct criterion for an optimal image during differential focusing. Deviation from ideal focus within ± 0.5 D is demonstrable by these means or by the use of cerebral-evoked potentials (BERKLEY and WATKINS, 1973). Unfortunately, none of these investigations provide information about the refractive state of the cats before contact lenses were fitted; the spectacle power required for best focus need not therefore represent the refractive state of the effective image plane in the normal animal. Single-unit refraction (HUGHES, 1977b) suggest the effective image plane to be emmetropic in the rat, but the great depth of field of small eyes when the pupil is constricted limits the sensitivity of the method, and aberrations preclude its use with a large pupil.

Emmetropia at the effective image plane of overtly hypermetropic eyes has, however, been demonstrated in nonmammalian species, such as pigeon, by means of an ERG criterion (MILLODOT and BLOUGH, 1971), for the frog by the refraction of single units stimulated with moving stimuli (MOSER and KRUEGER, 1972; MOSER, 1973), and by the determination of single-unit acuity thresholds in the fish (MEYER and SCHWASSMANN, 1970).

The necessary conclusion from GLICKSTEIN and MILLODOT'S (1970) hypothesis, that the fundus reflex originates at the vitreous/retina junction, receives little support in the literature. Alternative suggested sites have been the choroid (WALLS, 1942), BRUCH'S membrane (WEALE, 1966), or the pigment epithelium (FRY, 1967), but all of these lie behind the effective image shell and would lead to an apparent universal myopia, not hypermetropia. According to CAMPBELL and GUBISCH (1966), if polarised light is used to illuminate the fundus, then some 20% of the reflex is depolarised with a red cast, which suggests it to have penetrated the choroid. WEALE (1966) claims that bleaching of the photoreceptor pigments reduces the reflection of the polarized and depolarized components alike so that they must both arise beyond the photoreceptors. In contrast, however, RÖHLER et al. (1969) describe the depolarized reflex component as arising forward of the receptor layer, in the manner required by the above hypothesis, but it should be noted that this component forms a relatively small proportion of the reflex. Recent confirmations of VALENTIN'S (1879) report that the retinal refractive index is larger than that of the vitreous (NORDENSEN, 1934; AJO, 1949) established that a specular reflection must occur at the vitreous/retina interface. MILLODOT (1972) has computed this to be 0.06% of the incident beam, about 50% of the proportion actually recorded in man, so that the calculated front surface reflection explains 70% of the total human specular reflex. In a detailed discussion of this problem, MILLODOT (1972) fails to account for WEALE'S (1966) claim that pigment bleaching influences both specular and diffuse components of the reflex; this must be done before the subject can be regarded as even partially resolved.

The fundus reflex employed for retinoscopy in the cat is commonly regarded as originating at the highly reflective tapetum (WEALE, 1953; BONDS et al., 1972). This layer is separated from the outer limiting membrane, or presumed effective image shell, by a distance of some 50 μm which corresponds to a refraction of

0.35 D, but, because the tapetum lies behind the posterior focus, overt myopia would be expected rather than hypermetropia. It remains to be determined whether the dynamic refraction of the anesthetized cat is sufficiently hypermetropic to mask this apparent myopia or whether a significant component of the reflex arises from a region in front of the posterior focus.

Evidence that the retinoscopic reflex does arise at the retina surface has only been put forward for the rat (HUGHES, 1977b). An objective optometer was employed to show that the refraction of the surface nerve fibers and blood vessels is at 8.9 D, in good agreement with the standard retinoscopic refraction of 9.4 D, when the pupil is small. The reflex employed in retinoscopy is thus concluded to arise close to the retina/vitreous junction. The photoreceptor layer could not be directly refracted, but a mean of −2.1 D was determined for the orange choidal vessels which lie in the pigment cell layer. The presumed effective image plane lies some 0.036 mm vitread of the pigment layer, which is equivalent to a 2.5 D change in refraction (HUGHES, 1977b). The refraction of the image plane is thus about +0.5 D and indicates the eye to be close to emmetropia, in contrast to claims that the rat is functionally an extreme hypermetrope (MASSOF and CHANG, 1972).

The implication of GLICKSTEIN and MILLODOT'S theory that retinoscopically hypermetropic species are behaviorally emmetropic is thus substantiated to some extent by the technique of refracting the effective image plane, but evidence for the retina/vitreous junction as the site of origin of the fundus reflex is limited. A few other reports conflict with the theory. SIVAK (1974) describes the mean refractive state of 6.5 D in the goldfish as being in agreement with the refraction of the photoreceptor plane, rather than that of the retinal surface as computed from measurements made on frozen sections of the eye. In this instance, however, a simple calculation reveals that a 0.07 mm change in length of the globe is equivalent to a 1 D change in refraction. Loss of ocular pressure or vitreal expansion upon freezing are just two possible sources of substantial dimensional change capable of introducing considerable error into the reconstructed refractions. The computation of the refractive state of a small eye with any useful reliability requires extraordinary accuracy of measurement. Again, SUTHERS and WALLIS (1970) describe the 1.68 mm-long eye of the bat *Myotis* to be only 10 D hypermetropic as determined by retinoscopy, rather than some 65 D calculated from the great retinal thickness relative to the posterior focal length of the eye. No explanation of the discrepancy is available, but it may arise in the difficulty of refracting such small eyes.

2. Peripheral Refraction

It may no longer be true to describe the hemispheric field of view of the eye as

> wider than that of any optical instrument

(HELMHOLTZ, 1924), but its extent remains impressive. Yet even in man there has been little attention paid to the refraction of the uniocular field peripheral to the optic and visual axes.

It is not satisfactory to treat peripheral rays which pass through the dioptric system at considerable obliquity to the optic axis as if there is a single focal image

shell which may coincide with the effective image shell. Because of oblique astigmatism, such rays give rise to tangential and sagittal image shells (BENNETT and FRANCIS, 1962; SOUTHALL, 1964) which bridge the shell of least confusion and also, near the visual axis, the retina. More complex phenomena which appear in systems with finite aperture, such as asymmetrical coma, may be treated analytically by Seidel's formulae (SOUTHALL, 1964), but recourse must be taken to ray tracing for the consideration of even moderate physiologic obliquities, especially in view of the nonhomogeneous structure of the lens. In the absence of any analytic treatment of the oblique peripheral rays of the vertebrate eye, it is unjustifiable to hold a priori expectations of the peripheral refraction. The retinal image of the human eye has, however, been reported to be stigmatic only within 10° of the visual axis (FEREE and RAND, 1932); beyond this eccentricity even axially emmetropic eyes demonstrate astigmatic errors of great variety. At an eccentricity of 55°–70°, the unpractised eye has been described as benefiting little from the correction of these refractive errors (DOBREE and WEALE, 1954; MILLODOT et al., 1975); however, LEIBOWITZ et al. (1972) obtained improvement of peripheral motion sensitivity after the correction of peripheral optics. Although up to 8 D of spherical and 2.25 D of cylindrical correction could be necessary, certain subjects required less than 1 D correction some 60° eccentric which indicated that peripheral vertical or horizontal ametropia is not a *necessary* outcome of the dioptric structure of the eye.

A recent investigation of peripheral refraction (MILLODOT and LAMONT, 1974) which employed retinoscopy, refractometry, and subjective refraction confirmed the observations of FEREE and RAND (1932) and reported marked peripheral astigmatism. The ametropia was less than theoretically predicted (LE GRAND, 1967), not because of corneal flattening, so it would appear that peripheral aberrations are indeed to some degree minimized by adjustment of the SIEDEL coefficients of the nonhomogeneous lens.

It is essential to note that off-axis retinoscopy is more complex to interpret than on-axis retinoscopy, and caution is required in accepting published results (KEATING, 1975).

The possible importance of peripheral optics in species other than man was recognised by JOHNSON (1901):

> In our eye, possessing only a small angle of acute vision, a blurred image produced at a point near the periphery is of no consequence, but in the case of those animals which have a widely extended sensitive area and need to see all around them, a sharp focus for peripheral rays is of much greater importance.

Not only species with an extensive visual streak and lateral eyes like the rabbit ($\lambda = 77°$) but also those with more limited areas set at a considerable angle to the optic axis, rat ($\lambda = 60°$) and goat ($\lambda = 47°$) may require good peripheral optics. The goat area centralis is obviously organised as a region of very acute vision with its peak ganglion-cell density of 15000 cells/mm^2 (HUGHES and WHITTERIDGE, 1973) in spite of the great obliquity of its visual axis relative to the optic axis. The problems of oblique imagery may have been solved in such eyes, because there is *no* analytic demonstration that this is impossible. Alternatively, it may suffice for the majority of mammals with lower acuity than primates that central on-axis imagery is of such quality, in spite of a deterioration with increasing eccentricity that the most peripheral images remain adequate to the needs of the neural

apparatus. This is a problem in comparative optics which remains to be investigated, but such results as are available have been obtained by the modulation transfer function technique and will be dealt with subsequently.

At present there have been no systematic investigations of peripheral image quality and refraction in any mammalian species. Small changes of the refractive state across the pigeon retina have been reported by MILLODOT and BLOUGH (1971), but we have seen that these need not represent the refractive state at the effective image shell. Ray traces based upon oversimplified schematic eye assumptions (NYE, 1973) cannot provide support for these observations. Care must be taken before attributing teleologic significance to such gradients of refractive state. In the rat it is found that optometric refraction of the temporal retina along the visual axis reveals some 5 D of hypermetropia rather than the 9 D at the retinal surface observed along the optic axis. Gross examination of the eye indicates, however, that the retina is only two-thirds of its central thickness in the corresponding temporal region, so that the systematic retinoscopic error is smaller, and the observed refractions are compatible with emmetropia at the effective image shell even in the peripheral retina (HUGHES, 1977b). In the rabbit, DE-GRAAUW and VAN HOF (1977) claim the anterior field to be myopic in contrast to hypermetropia on the optic axis. However, HUGHES and VANEY (1977) find both wild and laboratory rabbits to a evince a slight hypermetropic refraction in the pigment layer from the binocular into the temporal field at the level of the visual streak. This finding is in keeping with the electrophysiological refractions of MEYER et al. (1972) which indicated near emmetropia over the whole field.

An asymmetry of the lens position in the eye, or a difference in the distance from the center of the lens to the peripheral and central retina, should not, of itself, be assumed to necessarily imply a difference in the refractive state of these regions. Such an assumption is implicit in discussion of the ramp retina of the horse (NICOLAS, 1930; DUKE-ELDER, 1958) and would be true if the focal length of the dioptric system were constant with varying eccentricity as is implied by MILLODOT and BLOUGH (1971) for the pigeon. However, in cat (VAKKUR et al., 1963; HUGHES, 1976a) and rabbit (HUGHES, 1972) the distance between lens and retina is reduced by about 10% towards the periphery but is accompanied by a change of PND, and thus no substantial alteration of refraction need be expected.

A further complication in assessing variations of refraction with retinal eccentricity is possible in species with lateral eyes and accommodation along the visual axis. MEYER and SCHWASSMANN (1970) describe the refraction of the bass *Paralabrax* as emmetropic in nasal, central, and temporal retina when the fish is paralysed with Flaxedil. Under Tricaine anesthesia, the lens moves forward, leaving the central retina emmetropic but bringing the temporal retina to −13 D of myopia and the nasal retina to a complementary refraction of 10 D of hypermetropia.

3. Epilogue

The great variation in the degree of retinoscopic hypermetropia which has been established among the mammalian species thus appears to represent a remarkable uniformity of functional mean emmetropia. Among the vertebrates in

general, the current acceptance of teleost refraction as hypermetropic rather than myopic leaves the lamprey eye as the last alleged instance of static myopic refraction with active accommodation for distance vision (FRANZ, 1934; WALLS, 1942). There is no evidence for specialization of the refractive state with relaxed accommodation for a specific life style or habitat. These studies are, however, based upon the refractive state under a cycloplegic, deep sleep, or death, and the physiologic accommodatory condition of rest (WESTHEIMER and BLAIR, 1973) may be quite different; in contrast to the static refraction, it may evince correlations with life style or size of a given species. The little information available on this topic is outlined in Section IV.

IV. Accommodation

1. Range of Accommodation

The ability of the young human eye to increase the refractive power of its dioptric apparatus by some 15 D during accommodation for nearby objects has attracted considerable interest over several centuries, so that an enormous body of literature has accumulated which incorporates much comparative material. Confirmation of a great deal of this information by modern techniques is badly required. The comparative study of a mammalian accommodation has been relatively neglected, and our knowledge of its range has changed little since the studies of HESS and HEINE (1898) and KAHMANN (1930).

Apart from man, the monkey possesses the greatest range of accommodation so far established among the mammals. HESS and HEINE's (1898) report of some 10–12 D of accommodation is substantiated by 12 D obtained upon brain stimulation (JAMPEL and MINDEL, 1967), 11 D from parasympathetic stimulation, and a claimed 28 D from drug action (CHIN et al., 1968).

The accommodation of the cat eye remains the most extensively studied after that of man. HESS and HEINE (1898) found the mean refractive state of the anesthetised cat to change by some 2 D upon electrical stimulation. A 3.5 D range was described by HARTRIDGE and YAMADA (1922) after examination of the influence of atropine and eserine on the refractive state—more recently the latter agent has been reported to induce some 8 D of accommodation (IKEDA and WRIGHT, 1972). Autonomic stimulation has revealed a wide variety of accommodatory ranges in the cat, 4–5 D (OLMSTED and MORGAN, 1941), 6 D (ARMALY, 1959), and even 11.5 D (MORGAN et al., 1943; OLMSTED, 1944); behavioral testing suggests some 3–4 D (BLOOM and BERKELEY, 1976). By contrast, the dog is reported to evince only about 1 D of accommodation (HESS and HEINE, 1898; ROBERTS, 1956).

Neither BARRETT (1898) nor HESS and HEINE (1898) were able to demonstrate accommodation in the rabbit, although some 2–4 D were claimed to be detectable in movements of the Purkinje images induced by the electrical stimulation of the freshly enucleated globe (SMITH, 1898) or, more recently, upon the stimulation of the sympathetic supply to the eye (OLMSTED and MORGAN, 1941). MEYER et al. (1972) were unable to obtain evidence of accommodation when employing single-unit refraction in conscious rabbits; the minimum visibile was constant for distances greater than 45 cm at an unknown pupil size.

Accommodation has not been demonstrated in the rat. LASHLEY (1932) concluded that it is not present because of the absence of a well-developed ciliary muscle in this species. The very small pupil of the rat can endow it with great depth of field under photopic conditions (BLOCK, 1969), and this has been demonstrated to be functionally significant by single-unit refraction and consideration of behavioral performance (HUGHES, 1977b).

Away from the common laboratory species, our information is even more limited. Rodents and ungulates in general are described as lacking accommodation (KAHMANN, 1930; WALLS, 1942; DUKE-ELDER, 1958) although apparently with little experimental basis. PRINCE et al. (1960) draw attention to the conventional ciliary apparatus of the ungulates. In a comparative examination of the ciliary muscle, WOOLF (1956) agrees with ROCHON-DUVIGNEAUD (1943) in describing it as well-developed in the ungulates and primates although effectively absent from the majority of rodents. WALLS (1942) resolves the paradoxical presence of an extensive ciliary muscle in ungulates which allegedly lack accommodation by concluding that the lens is too stiff to alter its shape significantly, but, as we shall see, this does not preclude the possibility of an alternative arrangement in these mammals. It will be obvious that there is a need for a fresh examination of this topic.

It is possible that the description of the "ramp retina" in the horse (WALLS, 1942; DUKE-ELDER, 1958) has reduced interest in the dynamic accommodation of herbivorous species because of its seeming redundancy. The "discovery" of the ramp retina is commonly attributed to NICOLAS (1930), but, in fact, it appears to have been derived from his data by WALLS (SIVAK and ALLEN, 1975). He pointed out that the ground surface at decreasing distances projects systematically at increasing elevations in the effective image shell and suggested that the lens-to-retina distance varies in such a fashion as to ensure the degree of myopia at a given elevation appropriate for focussing the region of the object plane, which gives rise to the local image.

The asymmetry of the horse eye has recently been confirmed (SIVAK and ALLEN, 1975), but the lens-to-retina distance is relatively uniform in the upper eye and the ramp unverified. However, these authors assume that the refractive state of the eye along a given axis is related to the corresponding PND, or its approximation, when in fact they may vary independently. The retinoscopic assessment of the horse eye (SIVAK and ALLEN, 1975) indicated no more than 1 D variation of refraction over the vertical field, but, again, the refractive state of the effective image shell may vary more or less than this. A serious difficulty is that an asymmetry sufficient to produce a gradient of only 1 D, or even a depth of field equivalent to this, would suffice to provide satisfactory imaging of objects from 1 m to infinity. Much more sophisticated testing would be required to establish whether a ramp retina is functionally present. There has never been any suggestion that the ramp retina operated for frontal vision along the fixation axis of the horse; it is possible that the moderate development of the ciliary muscle (PRINCE et al., 1960) suffices for the adjustment of focus in the anterior field.

The continuous assessment of the accommodatory state has recently been achieved for the human eye by the use of the infrared optometer (CAMPBELL and ROBSON, 1959) and subsequently, by the same technique, for the conscious pretri-

geminal cat (ELUL and MARCHIAFAVA, 1964). The static refraction of the sleeping or anesthetized cat eye was found to be 1.5 D, but upon waking it changed by −0.5 D to +1.0 D. Some 3–4 D of accommodatory power then remains to deal with objects up to 20 cm from the eye. It is claimed that the conscious cat evinces a decrease in its refractive power from the condition of rest when looking to the distance, 6 m. The physiologic tonic refractive state of the cat eye thus appears to be myopic in contrast to the hypermetropic anatomic condition of rest (WESTHEIMER and BLAIR, 1973) which can be determined under a cycloplegic or after death. The interpretation of ELUL and MARCHIAFAVA'S (1964) results in terms of the state of focus at the effective image shell is complicated by the factors discussed previously in relation to the static refraction of the cat.

WESTHEIMER and BLAIR (1973) find the refractive state of the monkey to be myopic when the visual field is empty, but, curiously, during sleep and anesthesia this changes to more pronounced *myopia* rather than to hypermetropia as in the cat under the same conditions. In man, the physiologic accommodatory resting state is similarly about −1.0 to −1.5 D under empty field conditions (CAMPBELL, 1953; TOATES, 1972) and when the pupil is small (HENNESSY et al., 1976) the accommodatory system rests in focus close to the hyperfocal distance.

2. The Mechanism of Mammalian Accommodation

The foundation of modern understanding of the human accommodatory process lies in LANGENBECK'S (1849) use of the Purkinje images to demonstrate its origin in the change of shape of the lens. In HELMHOLTZ'S (1924) view, the contraction of the ciliary muscle relaxes the zonular fibres and reduces tension on the lens capsule so that its inherent elasticity acting upon the matrix induces a more spherical shape; the excised lens thus assumes its form of greatest power. FINCHAM'S (1937) observation that the *decapsulated* human lens takes up the unaccommodated form led WEALE (1962) to put forward the current theory in which the lens matrix is regarded as possessed of its own elasticity, overcome by the capsule during accommodation, which tends to return the lens to an unaccommodated form. The work of FISHER (1969a, 1969b, 1971, 1973) has outlined in most elegant fashion the respective roles of the capsule and matrix in defining the properties of the human lens.

The monkey lens has not been investigated by FISHER, but the range of accommodation of this animal, its endowment with ciliary muscle, and the lens shape indicate the presence of an accommodatory mechanism similar to that of man. Support for this view is available from VAKKUR (1967), who finds the monkey schematic eye to be some 19 D myopic when based upon the dimensions of the excised lens—a refractive state consistent with the excised lens having taken up its accommodated form.

Fortunately, FISHER (1969a, 1971) has also applied his techniques to the examination of the rabbit and cat lenses. The value of Young's modulus of polar elasticity for the adult cat lens is 21 times and that of the young rabbit 5 times that for the human lens (FISHER, 1971). This lack of compressibility in conjunction with the low capsular energy of the cat and rabbit lenses (FISHER, 1969b) makes an accommodatory change of lens shape in these animals impossible on mechani-

cal grounds alone. The same conclusion almost certainly applies to the lens of the rat, which is even more spherical and contains a solid core. In contrast to the monkey schematic eye, those of the cat (VAKKUR and BISHOP, 1963), rabbit (HUGHES, 1972) and rat are all close to emmetropic when constructed from the dimensions of the excised lens, a result consistent with Fisher's observations.

The evidence for accommodation in the rabbit is poor, but the cat is undoubtedly capable of changing its refractive state in spite of its stiff lens. From their cat schematic eye, VAKKUR and BISHOP (1963) concluded that a change in lens shape and power would be a relatively inefficient means of altering the refractive state of the eye. The forward movement of the principal planes subsequent to such a change of shape would be more effective but is, of course, precluded by FISHER's results (1971). Their suggestion that the lens may translate in toto during accommodation appears to be the true foundation of the process in the cat.

The forward movement of the lens anterior pole during parasympathetic stimulation was measured by O'NEILL and BRODKEY (1969) in the cat and found to amount to some 0.6 mm at most; in a later paper (O'NEILL and BRODKEY, 1970) this estimate is reduced without explanation to 0.3 mm. The larger of the two estimates would amount to some 2 D of accommodation (VAKKUR and BISHOP, 1963) if it entirely represented translation of the lens rather than change of shape. Apparently larger displacements of the lens were observed by ARMALY (1959) during parasympathetic stimulation. The bulging forward of the pupil during accommodation in the *conscious* cat has been reported by HUGHES (1973), and its magnitude is consistent with the known range of cat accommodation if achieved by translation. Support for VAKKUR and BISHOP'S hypothesis thus arises at present from the argument that change in the shape of the cat lens is mechanically impossible, rather than a direct demonstration that axial translation occurs. A recent investigation has now shown only very small changes in the power of the cat lens subject to circumferential forces thus confirming the above arguments (SUNDERLAND and O'NEILL, 1976).

KEPLER (1611) suggested that the human eye achieves accommodation by axial movements of the lens. Calculation from GULLSTRAND'S schematic eye readily reveals that a 2 mm forward movement of the lens changes the refractive state of the human eye by only 1.24 D, so that the contribution of this mechanism to the total accommodatory power could only be small. Although the front surface of the human lens is known to move forward by some 0.3 mm during accommodation (FINCHAM, 1937), this is usually regarded as a result of change of thickness and curvature. Recent slit-lamp results of PATNAIK (1967) suggest that in fact the core centre may also shift forward by some 0.17 mm under these conditions, although it is still not certain that this arises from equatorial translation rather than lens-matrix redistribution. The classic experiment of HENSEN and VÖLCKER (1868) demonstrated the forward movement of the ciliary body in cat, ape, and man during accommodation, but this translatory motion would appear to be more effectively conveyed to the lens in the cat than in the primate eye. It is consequently of great interest to note that the anatomy of the ciliary regions is very different in cat and man (Fig. 14) (KAHMANN, 1930; WALLS, 1942; ROHEN, 1952, 1964), but in the absence of a comparative mechanical analysis, no functional interpretation of the dissimilarities can be made. It is doubtless pertinent,

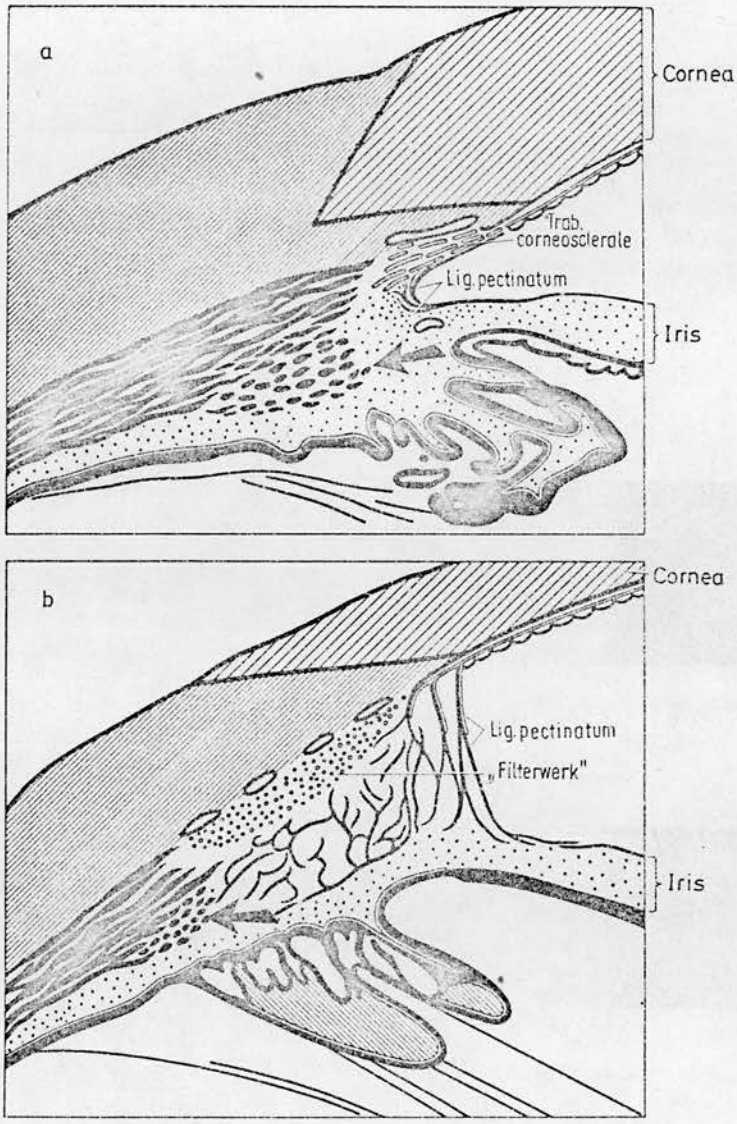

Fig. 14. Ciliary region of primate (*a*) and carnivore (*b*, cat). The transversely cut, circular muscle fibers are abundant in the former but weakly developed in the latter whose accommodation appears to be achieved by axial translation of the lens alone. (Courtesy ROHEN, 1964)

however, that the cat ciliary body is predominantly equipped with the meridional or longitudinal fibers of BRÜCKE (PRINCE et al., 1960; ROHEN, 1964), which are so appropriately oriented for the anteroposterior translation of the lens. In man it is the circular MÜLLER's fibres which predominate: these are very sparse in the cat.

Unless the cat ciliary muscles deteriorate with age, it would appear that the difference between its accommodatory mechanism and that of man must make us doubt WALL's (1942) claim that the cat

> Has but half the accommodation of a thirty year old man and loses even this in old age.

3. Epilogue

The elimination of corneal power when the fish eye is under water makes the position of the lens vertex especially easy to monitor and convenient for the study of accommodation under relatively natural conditions. In both elasmobranchs (NICOL, 1963) and teleosts (BREIT, 1957; PUMPHREY, 1961), accommodation appears to occur by displacement of the lens. The lens of the rock bass moves in a rostrocaudal direction during accommodation so as to alter the refraction of the frontal field (SIVAK and HOWLAND, 1973). Behavioral testing can elicit the entire 28 D range of accommodation which may be pharmacologically induced in this species (SIVAK, 1973). The alewife and silverside have been described as possessing up to 18 D of accommodation (BAYLOR and SHAW, 1962)—a range again very substantial in comparison with that of most mammals. CHARMAN and TUCKER (1973) have argued, however, that the goldfish and some other teleosts may not require an accommodatory mechanism because of the depth of focus of the eye.

Little reliable evidence of accommodation is available for birds, but it is claimed to be well developed among the diving species in which it is employed to offset the loss of corneal power when submerged. The dipper is described as possessing a cornea of some 40 D power and 48 D of accommodation (GOODGE, 1960); the robin has only 7.5 D of accommodation, but this is respectable in comparison with the range in mammals.

Among the fishes (TAMURA, 1957; SIVAK, 1973) and birds, it has been suggested that the magnitude and axis of accommodation vary according to feeding habits and life style, but our knowledge of the accommodatory powers of mammals is so limited that little can be said of such correlations. The otter is reputed to possess the greatest accommodatory power of the mammalian subprimates for the same purpose as the diving birds (WALLS, 1942; ROCHON-DUVIGNEAUD, 1943; DUKE-ELDER, 1958), so that it is able to maintain a similar acuity in air and water (SCHUSTERMAN and BARRETT, 1973). By contrast, the more aquatic sea lion eye is emmetropic in water and depends upon a flattened cornea and stenopaeic aperture for the formation of a good image in air (WALLS, 1942; SCHUSTERMAN, 1972). The range of accommodation among the seriously investigated mammals appears to follow the extent of their praxic skill. It is greatest in monkey, less evident in the paw-dominated cat, feeble in the dog, and apparently absent from the nonmanipulative rabbit.

WALLS (1942) lists several mechanisms whereby image quality can be made relatively independent of object distance in species lacking a dynamic accommodatory system. Of these, doubt has already been cast in previous sections on the ramp retina and the usefulness of elongated receptors. The stenopoeic aperture is another matter and is a definite asset under photopic conditions. The rat possesses no discernible ciliary muscles (LASHLEY, 1932; WOOLF, 1956) but is yet concerned with viewing at short distances and handles objects. The absence of accommodation is only behaviorally significant if the retinal image quality for the range of distance significant to that species is substantially worse than the *neural*, not the photoreceptor, "grain" employed in the specific acuity task considered. Under photopic conditions, the tiny pupil of the rat ensures such small blur circles that this does not occur, and its eye possesses an enormous depth of field

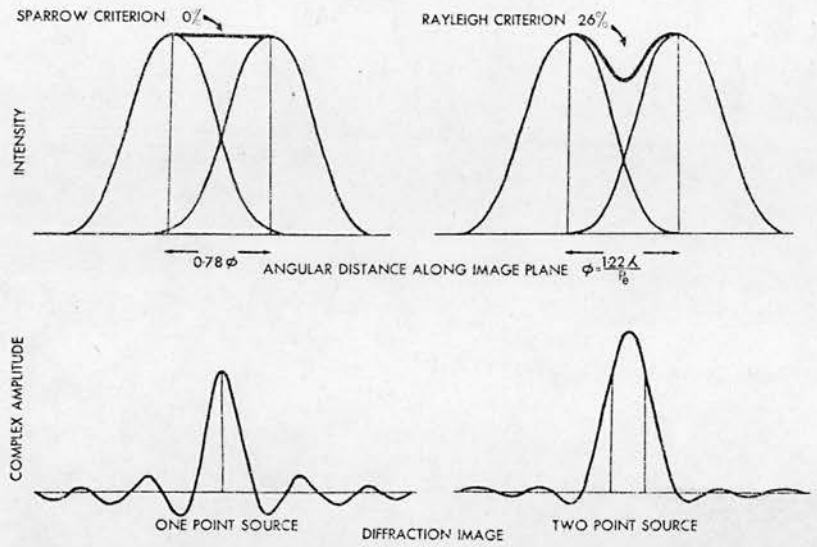

Fig. 15. Summed intensity distribution for the PSF of two points separated by distances appropriate to the SPARROW criterion and the RAYLEIGH criterion. It is to be noted that shape of PSF for one point remains quite different from that for two, even when they are closer together than suggested by the SPARROW criterion, and the central trough is absent

(HUGHES, 1977b). A curious but significant outcome of the dynamic accommodatory process in man (MOSES, 1970; ÉNOCH, 1975) and cat (VAN ALPHEN, 1961) has recently been demonstrated to be stretching of the retina with consequent change in the spatial direction associated with a given retinal locus.

V. Image Quality

The contents of the object space within the field of view of an optic system may be regarded as if formed by arrays of point sources of given luminance; their conjugate image may correspondingly be regarded as compounded from the elementary images of these point sources. Even in an ideal optic system, however, the image of a point source is not stigmatic because the inevitable presence of a finite aperture ensures a diffraction pattern consisting of a central Airy's disc concentric with a series of light and dark rings. The intensity distribution across the central disc is Gaussian and represents the pointspread function (PSF) of the exit pupil of the optic system (see WESTHEIMER, 1972, 1973, and FRY, 1970, for theoretical treatment). The dimensions of the PSF thus limit the amount of object-space detail which may be represented in the image space; the images of two points separated by less than 0.78 of the PSF radius, show only a single intensity peak (SPARROW, 1916) (Fig. 15). The angular diameter of the first zero of the PSF, as subtended from the exit pupil, is given in radians by $2.44\lambda/p_e$, where λ is the wavelength of the light when passing through the optic media in nm and p_e is the exit pupil diameter in mm. In real optic systems, however, the pointspread func-

tion width varies inversely as the pupil diameter only over limited range; above this it increases in size with the pupil. Focus error, aberrations arising with the larger pupils, and light scatter in the optic media compound with the effects of diffraction to generate a pointspread function with a Gaussian core, which closely matches the ideal diffraction image in man when the pupil is small (CAMPBELL and GUBISCH, 1966), and an exponential skirt which represents the influence of all other factors. The pointspread function is thus a useful end product by means of which the overall quality of an optic system may be judged in terms of object-space resolution under given conditions.

Just like any other two-dimensional signal, the PSF may be represented as compounded from sinusoidal Fourier components at different orientations. The finite width of the PSF ensures that, unlike the Dirac delta function employed in systems analysis, its Fourier spectrum covers only a finite spatial-frequency range. Widening of the PSF along a given diameter thus corresponds to the failure of the optic system to transmit high spatial frequencies of the corresponding orientation; the Fourier transform of the PSF specifies the bandpass range, or modulation transfer function (MTF), of the system. This function displays the ratio of contrast in the image to that in the object for the spatial frequencies below the cut-off frequency of the system. It is a convenient approximation related to the Rayleigh criterion to assume the half-height width of the PSF as equal to one period of the Fourier component at the cut-off frequency.

The PSF and MTF are thus inverse transforms and may be obtained from one another by calculation if the PSF is rotationally invariant; otherwise the MTF is a complex function, the phase factors of which must be taken into account if gross errors in the PSF and subsequently calculated image distributions are to be avoided (RÖHLER and HILZ, 1965). Only for grating images can rotational invariance be safely ignored in such calculations.

The image quality of the human eye was first adequately established by FLAMANT (1955), who projected a line of light onto the retina and measured the intensity distribution across its aerial image formed in front of the eye by rays reflected from the fundus. The measurement of the linespread function (LSF) is technically easier than that of the PSF because of the greater amount of light available. The square root of the double-pass LSF transform is required to specify the system performance as its single passage MTF. The aerial image technique has been technically improved by various workers (PSF determination, RÖHLER, 1959, 1962; LSF, WESTHEIMER and CAMPBELL, 1962; CAMPBELL and GREEN, 1965) to culminate in the work of CAMPBELL and GUBISCH (1966), who regard the 1′ half-height width of the LSF core as determined by the diffraction image width alone at the optimal 2.4 mm pupil diameter in man. The MTF has been directly established for man by projection of grating patterns onto the retina and measurement of their contrast loss (WESTHEIMER, 1963; RÖHLER et al., 1969) with results similar to those obtained by calculation from the LSF.

The aerial-image, double-pass technique was first employed for the cat eye by MARRIOT and MORRIS (1961) and WESTHEIMER (1962), but the pupils were dilated and a relatively poor image reported. The MTF was assessed from photographs of the retinal image of projected grating patterns by WÄSSLE (1971), and the calculated PSF found to be of 4′–5′ half-height width for a 3 mm pupil; the image

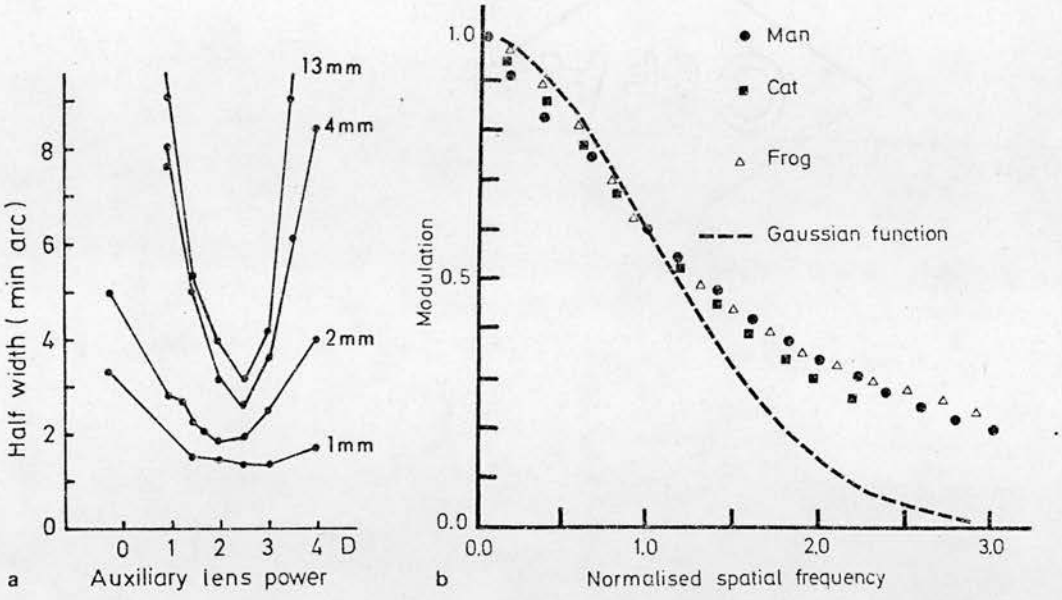

Fig. 16(a). Cat PSF half-height half-width for various degrees of defocusing and pupil size. (After ENROTH-CUGELL and ROBSON, 1975). (b) The normalized modulation transfer functions of man, cat, and frog are very similar in form but quite different from a Gaussian distribution. (After KRUEGER and MOSER, 1973)

quality of the cat eye is thus substantially poorer than that of man. Subsequent assessment of the cat LSF (BONDS et al., 1972; BONDS, 1974) confirm the findings of WÄSSLE (1971).

The results of these double-pass methods have been criticized by IKEDA and WRIGHT (1973) and ENROTH-CUGELL and ROBSON (1974) as leading to a spurious underestimation of resolving power. IKEDA and WRIGHT (1972) consequently substituted fluorescein angiography to make the smallest vessels of the retina a source from which to photographically obtain the single-pass LSF. For a 1.5 mm pupil, they observed a width at half amplitude of 4′—no better than WÄSSLE's double-pass result, yet obtained with a smaller pupil. IKEDA and WRIGHT (1972) claim, however, that the result is an improvement on previous double-pass findings, because they compare the half-width at half-height with previous values for the half-height width. WÄSSLE's (1971) results were again confirmed by the single-pass technique of ENROTH-CUGELL and ROBSON (1974), who employed a light guide which extends just beyond the retina to deliver light falling on the probe tip to a photocell when the image of a line source is scanned across it. The half-height width for a 3 mm pupil was 4.3′. Their results for a range of defocusing and pupil sizes are shown in Fig. 16 A, where the 1 mm pupil is accompanied by an LSF half-height width of 3′, the narrowest so far demonstrated for the cat.

Although the half-height width of the cat LSF is similarly described by various observers for equivalent conditions, the extent of the tail of the distribution has been subject to discussion. The LSF of WÄSSLE (1974) falls to zero at about 7′ radius, whereas BONDS (1974) describes a wider "skirt"; the agreement between

the results is very good when the animals with the best optics are compared, in that the LSF of BONDS (1974) is only some 3% of its peak amplitude at 7′ radius. That an extensive skirt does exist around the PSF and LSF has been demonstrated by means of an intraocular fiber optic probe by ROBSON and ENROTH-CUGELL (1975), who suggest that 20% of light entering the retina is scattered more than 15′ from its geometrically determined position. None of these studies take into account the standing zero frequency illumination which may result from the eye operating like an integrating sphere—possibly an important consideration when a tapetum is present as in the cat.

Both *single*-pass methods mentioned above establish the MTF of the optic system without incorporating the effects of transmission through the retina. In one instance, the retinal surface vessels act as a source, and in the other the probe extends beyond the retina. The problems of specifying the plane of origin of the fundus reflex, especially in the cat eye, make it difficult to assess the extent to which the retinal MTF is involved in the *double*-pass methods. In man, as we have seen, there have been substantial arguments that the fundal reflex arises behind the receptors (WEALE, 1966), so that the double-pass method may give rise to spuriously large values of LSF width because of scatter in the post-receptor layers. In the cat, however, the similarity of the single- and double-pass LSF half-height widths at equivalent pupil sizes suggests that such scatter may be of significance to resolution only in so far as it possibly broadens the PSF "tail." The same argument indicates that the retinal MTF plays little part in the determination of the overall optic quality of the living cat eye. This conclusion is supported by direct measurements of the retinal MTF of human (OHZU and ENOCH, 1972), squirrel monkey, and rat (OHZU et al., 1972). The human foveal MTF is superior to that for the axial optic system as determined by CAMPBELL and GREEN (1965) in spite of the use of material which had been deprived of a blood supply for 10 min and thus probably did not represent the optimal in vivo performance. The MTF of the squirrel monkey and rat retina was not grossly different from that of man and thus much superior to that of the optics in the latter species. The rat retinal MTF undergoes a precipitous decline in high spatial-frequency transmission between 2 and 11 min after the cessation of the blood supply (OHZU et al., 1972); the increased scatter appears to arise in the neurones of the retinal layers overlying the photoreceptors.

Of the remaining mammals a detailed MTF, measured shortly after death, is available only for the enucleated eyes of cow and pig (RÖHLER, 1962). The frog PSF is some 11′ wide at half amplitude (KRUEGER and MOSER, 1971, 1972) at an unknown pupil diameter, and the eagle LSF is about 1′ wide for a 6 mm pupil (SHLAER, 1972), which suggests that its optics are superior to those of man in whom the same LSF width is obtained only at smaller pupil diameters. This suggestion is substantiated by the observation (FOX et al., 1976) that at high luminances the falcon resolves a 160 cycle/° grating, whereas the human limit is 60 cycles/°. Such a performance by the bird requires an LSF width of some 22″ which is quite outside the human range. The shape of the frog, cat, and human MTF is very similar (KRUEGER and MOSER, 1973) but not fitted by a Gaussian curve (Fig. 16B). The similarity of the MTF of different species was assumed by HUGHES and WÄSSLE (1977) in order to obtain the rat PSF width at half ampli-

Table 3

	Man	Cat	Rat
PSF. half-height width for 3 mm pupil	1′	4–5′	30′
Width on retina	0.005 mm	0.018 mm	0.03 mm
Optimal PSF. half-height width for species	1′	3′	13′
Width of pupil	2.4 mm	1.0 mm	0.3 mm
Approx. ambient illumination for this pupil size (Fig. 17)	2.7 lg(cd/m^2)	2.5 lg(cd/m^2)	2 lg(cd/m^2)

Sources of data: man, CAMPBELL and GUBISCH (1966), WOODHOUSE (1975); cat, WÄSSLE (1971); optimal PSF. is smallest value from ENROTH-CUGELL and ROBSON (1974); rat, smallest size assumed optimal, HUGHES and WÄSSLE (1977).

tude from the cut-off frequency observed for a grating image projected onto the retina. The half-height width for a 0.33 mm pupil under photopic conditions was some 13′, which is about double the calculated diffraction limited value.

The power of the Fourier method for the overall description of optic systems (WARD and DAVIS, 1972) has not yet been extensively applied to comparative investigations. The systematic investigation of the influence of pupil size and defocus has begun for man (CAMPBELL and GREEN, 1965), cat (ROBSON and ENROTH-CUGELL, 1974; BONDS, 1974), and rat (HUGHES and WÄSSLE, 1977). The influence of oblique incidence has barely been touched upon; the results of RÖHLER (1962) enable estimation of the half-height width of the LSF for eccentricities up to 50° in man, and BONDS (1974) has presented LSF measurements ranging 30° either side of the visual axis in the cat. Both sets of results indicate a substantial peripheral deterioration in image quality; in the cat this finding is challenged by WÄSSLE (personal communication) from results obtained by the grating-projection technique. The interpretation of the peripheral observations on image quality is at present difficult, because the pointspread function is almost certainly not rotationally symmetrical for oblique rays, and the MTF should take on complex components (RÖHLER and HILZ, 1965). In addition, the studies of cats have been made with contact lenses in position, and no examination of their influence on oblique rays has been reported.

The variety of factors which influence the PSF and MTF make essential the standardisation of at least pupil diameter and focus when comparing the optic image quality of different species. If the resolving power of the optic apparatus is to be compared with behavioral acuity for a range of species, it is convenient to have the PSF specified in terms of its angular extent in the object space common to them all. From Table 3 it is apparent that between man and rat there is a 30-fold range of optic resolution, or PSF half-height width, when the pupil is 3 mm in diameter which alone indicates the difference in quality of the optical systems. Under these conditions, however, the differing PNDs' of the eyes ensure that they would not be operating at the same F_{no}. Discussions involving relative acuity might more suitably be served by comparison of the PSFs' when the pupil diameters are in the ratio of the PNDs' of the eyes concerned. In this instance, the rat with a 0.5 mm diameter pupil is to be compared to a man with a 3.0 mm pupil when their PSFs' differ only 13-fold in half-height-width. There is little evidence,

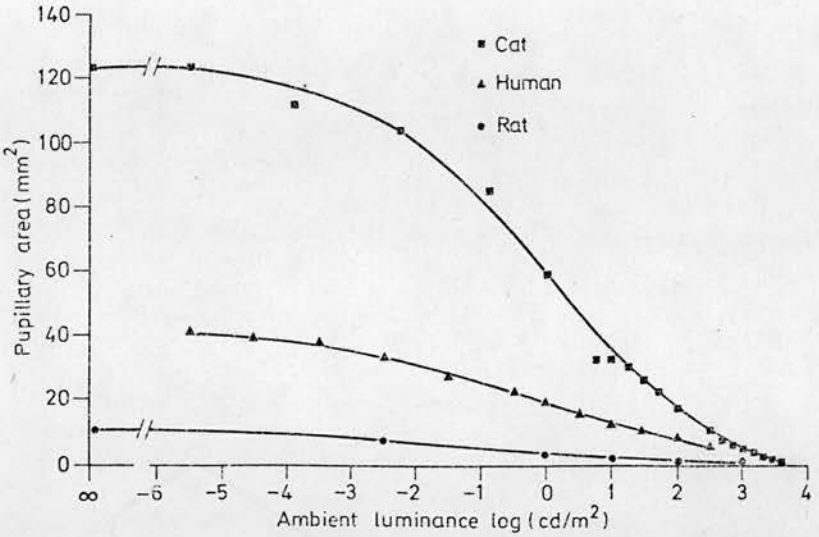

Fig. 17. Pupillary area as a function of light intensity for man, cat, and rat. Curves follow a very similar course with changing intensity. (After DE GROOT and GEBHARD, 1952; WILCOX and BARLOW, 1975; HUGHES, 1977c)

however, that different species operate at the same F_{no} over a range of conditions of illumination.

The opposing effects on the PSF half-height width of diffraction and aberration ensure that in man its value is minimal for a 2.4-mm-diameter pupil (CAMPBELL and GUBISCH, 1966). A similar minimum PSF width for a pupil diameter between 2 and 3 mm has been claimed for the cat (BONDS, 1974), but the results of ENROTH-CUGELL and ROBSON (1974) indicate a monotonic decrease down to 3′ for a 1-mm pupil; the smallest rat pupil tested, 0.33 mm, gives a minimum 13′ wide PSF at half-height (HUGHES and WÄSSLE, 1977). Resolution is thus optimal at quite different pupil diameters in these three species.

Under natural conditions, the pupil diameter is set by the pupillary light reflex, and an alternative means of comparing the optic performance of different species is to consider image quality at a given light intensity in a common environment. The optimal pupil sizes of man, cat, and rat are then revealed to be attained at similar photopic luminances characteristic of an external daytime environment of about 1000 cd/m^2 (man, DE GROOT and GEBHARD, 1952; cat, WILCOX and BARLOW, 1975; rat, HUGHES, 1977c).

The relationship between pupillary diameter and light intensity is of similar form for the investigated mammals (Fig. 17), but the pupillary area of cat and rat can change over a 135-fold range (BARLOW and WILCOX, 1975; HUGHES, 1977c), in contrast to the 10-fold range of man. At diameters other than that optimal for geometric optical resolution, it does not follow that the *performance of the system* is not optimal; quantum limitations on light flux may prevent attainment of the apparent geometric resolution unless the pupil size increases. The optimal diameter of the pupil in terms of physically achievable resolution thus changes with light intensity, even when the limitations of the neural apparatus are not taken

into account. The introduction of an artificial pupil larger or smaller than the *natural* pupil of man reduces resolution (CAMPBELL and GREGORY, 1960; WOODHOUSE, 1975) to some extent at all diameters. WOODHOUSE and CAMPBELL (1975) conclude from the small magnitude of this effect that the primary role of the pupil is not simply to establish optimal resolution.

The resolving power of the cat and rat is sufficiently low for their pupils to be able to contract to a much smaller size than in man before diffraction limits behavioral acuity. For such arrhythmic nocturnal species, this range permits rapid adaptation and greater contrast sensitivity in the early stages of dark adaptation when passing from light to dark. As WOODHOUSE and CAMPBELL (1975) point out, WALLS (1942) suggested that

> the slit pupil is thence in a sense paradoxical, for though it is an adaptation to nocturnality it has nothing whatever to do with seeing in a dim light

but now the paradox is resolved. The more limited pupillary diameter range of man confers similar advantages which have been argued to be of greater functional importance than optimisation of resolution (WOODHOUSE and CAMPBELL, 1975).

From a systems point of view, it thus appears that comparison of the image quality in different species requires full knowledge of its behaviorally encountered light intensity range under normal conditons. The striking influence of the ambient light intensity on behaviour patterns in forest and bush has been outlined for the nocturnal Malagasy *Lepilemur* (PARIENTE, 1974) in a model study representative of what is required for other species. It is obviously possible that the peripheral aberrations which come into play as the pupil dilates may be so adapted to the habitat and life style of each of a given group of species as to result in ecologically correlated variations of rank order of their image quality when the ambient light intensity is changed.

D. Retinal Topography

I. The Photoreceptor Layer

The discriminatory capacity of an animal at a given eccentricity from its fixation axis is potentially limited as much by the neural apparatus of the corresponding retinal region and subsequent stages of the central visual system as by the quality of the local retinal image. MÜLLER'S (1853) demonstration that the photoreceptors are the first stage of neural processing and potentially set the ultimate limitations on its performance was not long followed by SCHULTZE'S (1866) extensive comparative study of the retina of nocturnal and diurnal species, which established the duplex nature of the receptor layer—the rods serving scotopic and the cones photopic vision. The distribution of rods and cones within one retina may follow topographically similar or quite different patterns, but, so far, only a few mammalian species have been quantitatively examined.

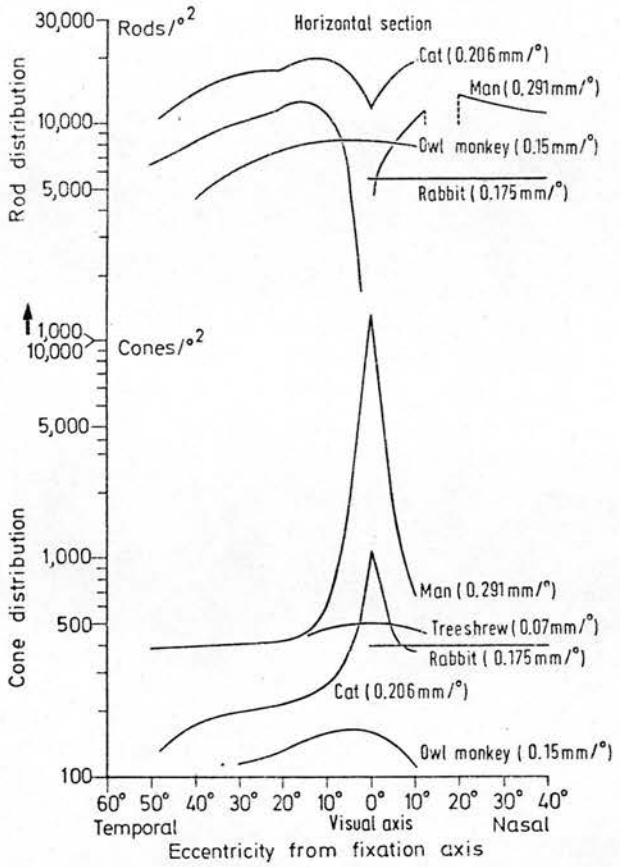

Fig. 18. Rod and cone densities/°² as measured in the horizontal plane about the visual axis of various mammalian species. Values were converted from published densities/mm² by means of the retinal magnification factors shown. Sources: man, ÖSTERBERG, 1935; tree shrew, ROHEN and CASTENHOLZ; rabbit, HUGHES, 1971; cat, STEINBERG et al., 1973; monkey, OGDEN, 1975

The maps of human receptor distribution provided by ÖSTERBERG (1935) clearly demonstrate the anatomic basis of HERSCHEL'S statement (BREWSTER, 1830) that

> a faint star ... will yet totally disappear, as if suddenly blotted out, when the eye is turned full upon it...

in the absence of scotopic receptors from the central fovea (Fig. 18). An increased cone density and correlated reduction in rod density occurs at the cat area centralis, as in the fovea of man, but the rod population is much less reduced as befits this nocturnal species (Fig. 18); such infiltration of the cones in the area is without detriment in the cat because of its lower photopic acuity than man. In the nocturnal owl monkey (Fig. 18) (OGDEN, 1975), not only are the rod and cone populations intermingled near to the fixation axis, but their distributions follow a similar course, and the relative proportions remain constant; absolute densities, however, differ considerably between the two populations. When a visual streak is present

in the retinal ganglion-cell layer, then the underlying photoreceptor distribution also shows increased density in a band-shaped region as in rabbit (Fig. 18) (HUGHES, 1971), cat (HUGHES, 1978), and turtle (BROWN, 1969).

Such duplex retinas form the majority of those encountered among mammalian species. Pure rod or cone retinas have been reported, but it is currently debatable whether such a description is strictly true for any mammal. The rat has been alleged to possess only rods (LASHLEY, 1932; MESSING, 1972), but several investigators identify cones (WALLS, 1934; SIDMAN, 1958; SOKOL, 1970) in the functionally useful concentration of 1:100 rods (HUGHES, 1977c). The tarsier retina is said to be of the pure-rod type (POLYAK, 1957; ROHEN and CASTENHOLTZ, 1967) but so small a proportion as an easily overlooked single cone per 1000 rods (KOLMER, 1930), a ratio found in the rod dominated retina of the lemuriform *Cheirogaleus* (ROHEN and CASTENHOLTZ, 1967), may be functionally important, because it can make a substantial contribution to diurnal acuity. The exclusively cone populations reported for the tree shrew (ROHEN and CASTENHOLTZ, 1967; WOOLLARD, 1926) and ground squirrel (DOWLING, 1964) have also been questioned; rods have been alleged in the former species upon the basis of light microscopy (POLYAK, 1957), and peripheral rodlike structures have been described in electronmicroscopy studies (SAMORAJSKI et al., 1966). The limited summation available from these reputedly small rod populations would bring their functional value into question, except that recent electronmicroscopy enables the differentiation of substantial numbers of the receptor population in some allegedly pure-cone retinas as a new rodlike class which might commonly be confused with cones under light microscopy (WEST and DOWLING, 1975). Such receptors form 40%, 10%, and 5% of the grey squirrel, prairie dog, and ground squirrel retinas, respectively, and show little centroperipheral change in proportion. The ERG b-wave threshold differs among these species in accordance with the "rodlike receptor" proportions. Reexamination of other rod- or cone-dominated retinas with the new methods appears to be in order.

The physiologic properties of the great majority of ganglion cells indicate that they receive both rod and cone inputs when they overlay the two receptor types in a given retinal region; cat (BARLOW et al., 1957a, 1957b; DAW and PEARLMAN, 1969; ANDREWS and HAMMOND, 1970a, 1970b), monkey (GOURAS and LINK 1966). Apart from the mesopic state (ANDREWS and HAMMOND, 1970a), a ganglion cell responds to just one receptor type, to rods under scotopic and cones under photopic conditions (GOURAS and LINK, 1966), with its receptive field size changing little. A small number of pure-rod receptive fields have been described in cat retina (ANDREWS and HAMMOND, 1970a), and pure-cone midget fields may be recorded from the perifoveal region of the macaque (GOURAS, 1971), but in general the double photoreceptor distribution maps into a single retinal ganglion-cell distribution. The topographic implications of this arrangement in terms of differences in photopic and scotopic resolving power, light sensitivity, etc., across the retina are dependent upon the unknown quantitative features of connectivity between the photoreceptors and ganglion cells.

It is often stated that, other than near a foveal pit, the retinal ganglion cell and underlying cone distributions follow each other closely. This is certainly true in the commonly considered duplex retinas which possess a diurnal cone dominated

area—man (OPPEL, 1965), macaque (ROLLS and COWEY, 1970), and cat (STEINBERG, 1973); in such species the rod distribution is inversely correlated with the ganglion-cell density, and the total receptor density is relatively uniform. Similarly, the retinal ganglion cell and receptor distribution across the supposedly pure-cone retina of the tree shrew parallel each other (ROHEN and CASTENHOLTZ, 1967). However, the area of the predominantly nocturnal duplex retina of *Aotes*, the owl monkey (OGDEN, 1975; ROHEN and CASTENHOLTZ, 1967), is accompanied by little change in rod, cone, or total receptor density, and yet the ganglion-cell distribution independently reveals a marked peak density (JONES, 1965); even in the supposedly pure-rod retina of the tarsier the retinal ganglion-cell density is substantially elevated at the fovea (ROHEN and CASTENHOLTZ, 1967) in spite of only a small receptor density increase. The alleged relationship between cone and ganglion-cell distribution is thus perhaps true for diurnal forms but is quite without general applicability.

Concentration on human foveal vision has led to an excessive emphasis in the literature on the limitations set by the photoreceptor matrix for visual resolution. The work of ÖSTERBERG (1935) has shown for the whole retina of man that 120 million rods and 6.5 million cones project to 1.2 million optic nerve fibers (POTTS et al., 1972), giving ratios of 95:5.4:1 for rod:cone:optic nerve fibers, respectively. Information available for the cat retina (STEINBERG et al., 1973; HUGHES, 1975a; HUGHES and WÄSSLE, 1976) indicates even greater overall convergence, with 204 million rods and 3 million cones projecting to 193000 optic nerve fibers and thus leading to 1000:15:1 for the rod:cone:optic nerve fiber ratio. Obviously gross overall ratios may mask local regions of lesser convergence, such as the 1:1 coupling of cones to ganglion cells at the primate fovea (BOYCOTT and DOWLING, 1969), but in general the potential upper limit set on resolution by the photoreceptor matrix cannot be approached, because there are usually not enough ganglion cells in any local region to relay the output of the corresponding receptor cells by "private" channels.

Several workers have sought quantitative details of local variation in receptor-to-ganglion cell ratios by means of gross local measurements of the thickness of the three nuclear layers of the retina (CHIEVITZ, 1889; ZURN, 1902; ROHEN and CASTENHOLTZ, 1967). Counts of the relative nuclear densities in central and peripheral retina have also been made for man, simians, prosimians, guinea pig, ground squirrel and rabbit (VILTER, 1949, 1954; OPPEL, 1965; ROHEN and CASTENHOLTZ, 1967; HUGHES, 1971). These ratios may be misleading if not corrected for thin-section sampling errors (ABERCROMBIE, 1946) but do indicate different classes of organisation of the central and peripheral retina which correlate with the balance of nocturnal and diurnal activity in the life style of given species. Such methods do not, however, permit the actual connectivity of the cells to be deduced, so that it would be possible for each ganglion cell to be connected to all overlying receptors in spite of a low convergence ratio.

Recent investigations of monkey (DOWLING and BOYCOTT, 1966; BOYCOTT and DOWLING, 1969; KOLB, 1970), and cat (BOYCOTT and KOLB, 1973) outer plexiform layers have begun the provide specific information about receptor-to-bipolar connectivity. Some 15–45 rods supply each rod bipolar in monkey, and a given rod may supply more than one such bipolar, whereas over much of the

retina a cone may supply a single midget invaginating bipolar, possibly a midget flat bipolar, and a flat bipolar which receives an input from about 7 other cones. The cat invaginating-bipolar contacts no fewer than 4 cones and up to 10, the flat bipolar from 8 to 14 cones, so that the potential for a fine cone-sampling-matrix appears to have been lost before the inner plexiform layer. The area of the rod and cone bipolar fields, the ratio and numbers in which the various bipolar classes project to the ganglion cells, and the variety of ganglion-cell classes at different eccentricities remain unknown until the details of the inner plexiform layer connections are worked out. Until then, our knowledge of relative scotopic and photopic resolving powers in any given region of retina must be arrived at from other considerations than the photoreceptor distribution.

Although receptor-to-ganglion cell convergence prevents the achievement of the receptor matrix potential for the accurate location of stimuli in visual space, it does not follow that the matrix resolution is totally lost. The discrete elements of the photoreceptor matrix may be employed with little convergence in the generation of functional subunits which precede the ganglion cells. Thus the rabbit has a behavioral acuity amounting to some 20′ at best, yet its directional units show differential response to stimuli separated by only 6′ (BARLOW and LEVICK, 1964), and the eye can track OKN stimuli moving at a rate of less than 1.8′/s (COLLEWEIJN, 1971; OYSTER et al., 1972). The technique of assessing visual acuity by means of the optokinetic response (CATFORD and OLIVER, 1973) thus gives values similar to those obtained by standard methods for central vision in man when convergence from receptor to ganglion cell is 1:1. In other species the acuity so determined is spuriously high compared with that determined behaviorally.

II. Retinal Organisation

1. The Area Retinae

That human oblique vision is less acute than central vision was well known by the time of KEPLER (1604); he attributed the difference to the combined effects of variation in retinal constitution and poor peripheral optics. The significance of the specialized region of retina bearing yellow pigment, the *macula lutea*, and the thinned retina at its center had not, however, been correctly interpreted as late as 1830 (BREWSTER, 1830), in spite of its location on the visual axis. Indeed, at that time, the region was thought to contain an aperture, the *foramen centrale*, which gave rise to the blind spot. Not until MÜLLER (1856) was the organisation of the *fovea centralis*, its significance in central vision and the possibilities for variation of organisation across the retina and between species fully understood. Subsequent investigations emphasized fine foveal receptors, rods in some species but usually cones, clearing of the bipolar and ganglion cells from the foveal pit and the absence of overlying blood vessels as specializations for high resolution vision in a wide variety of vertebrates (POLYAK, 1957).

The absence of a foveal pit from the localized concentration of specialized nerve cells and receptors encountered at the intersection of the fixation axis with

the retinas of investigated mammalian subsimians did not prevent MÜLLER (1861) from recognising their functional equivalence to the foveal elements as a means of improving local resolution: he described such regions as *central areas*. Among the mammals and most other vertebrates with nonfrontal eyes, such areas are not central but situated in temporal retina so as to form the visual pole of the forward fixation axis. For these regions, therefore, it is best to employ the term *area retinae temporalis*.

The macroscopic examination of the eye cup and microscopic study of radial sections from the retinas of a wide variety of species (CHIEVITZ, 1889, 1891; SLONAKER, 1897; ZURN, 1902; WOOD, 1917; BRÜCKNER, 1961a, 1961b) has since revealed two common forms of retinal ganglion-cell distribution which appear to be specialised for increased resolution, the usually round *area retinae* of MÜLLER and a "bandlike area" or *visual streak*, which extends horizontally across the retina. Similar classes of sensitive area were described upon the basis of ophthalmoscopic appearance of the fundus blood vessels in mammals (JOHNSON, 1901).

In the subsequent discussion, an *area retinae* or visual streak is assumed to be established by the presence of a locally increased ganglion-cell density; increased retinal thickness or photoreceptor density, the absence of overlying major blood vessels, or reduced convergence from receptors to ganglion cell may indicate or substantiate the presence of an area but do not define it. So far no mammal has been found to lack both an area and a visual streak.

This approach conflicts to some extent with that of ROHEN and CASTENHOLTZ (1967), who employ the extent of the change in primate local receptor to ganglion-cell convergence ratio in passing into the *area retinae* from the periphery to define a degree of "centralisation" (ROHEN, 1958). The foveate arrhythmic form, homo, or nocturnal species, tarsius, show obviously increased convergence in passing towards the fovea with ratios of 16:2:1 and 40:8:1, respectively (peripheral receptor: central receptor: ganglion cell) just as do the afoveate arrhythmic forms such as galago, 30:10:1. Among these species the centralization is even more obvious when the receptor data is divided into rod and cone components, and all are regarded as possessed of differentiated area retinae. Centralization in the tree shrew cone retina, 1.6:0.8:1, and cheirogaleus rod retina, 60:30:1, is less obvious and described as *„ohne differenzierte Netzhautmitte"* (ROHEN and CASTENHOLTZ, 1967), yet both cheirogaleus (WOLIN and MASSOPUST, 1967) and tupaia (Fig. 20c) possess area retinae which are clearly differentiated by an increase in ganglion-cell density. A parallel increase in receptor density masks the absolute increase in ganglion-cell density at the area when differentiation is judged only in terms of the local convergence ratio. The absence of centralization cannot therefore be equated with the absence of an area.

In some species, such as guinea pig and squirrel, the retinal ganglion-cell distribution is relatively uniform; depending upon its density, or preferably its angular resolution, such retinas are regarded as "universally peripheral" or "universally macular." It may be wondered why such organisation is not more common; why should an area centralis or visual streak be differentiated in other retinae? It will be appreciated, however, that all regions of the visual field are not necessarily of equal significance to a given species; a need for economy in usage of neural apparatus would therefore lead to differential organization of the retina.

Retinal uniformity is most conspicuously lacking in those species which manifest high visual acuity and whose area retinae set a disproportionately high demand on central tissues for the processing of their output. The sharply circumscribed extent of such retinal regions may thus be explained in terms of the incapacity of the CNS to make central provision for the output of an entire uniform high-resolution retina with mechanisms equivalent to those it can provide for a circumscribed area centralis. If the ganglion-cell density of the entire cat retina were the same as that at the peak of its present area centralis and cortical provision were to be proportionately increased, then the feline area 17 would need to be increased from 340 mm^2 in area to 50000 mm^2—5 times larger than the visual cortex of man! Given that a gradient of density is necessary in some species, then many different distributions are possible, depending upon the means by which sampling redundancy is minimised; some of these are discussed subsequently.

It does not follow, however, that the total sampling distribution across the retina is determined simply by considerations of resolution; the variety of receptive field classes present in the retina indicate that separate sampling distributions exist for other classes of information. However, the theoretical apparatus for treating such distributions is not available, and thus we confine the discussion to consideration of a system for spatial resolution such as is represented by the cat brisk-sustained class. Even in such a system it is necessary to consider sensitivity as well as spatial resolution when arriving at conditions for optimal sampling. Limitations on the independence of light sensitivity and resolution in an optimally organized system are set by the sampling theorem. Treatment of resolution in terms of the density of image sampling points neglects the finite area of the sampling apertures.

Consider an eye in which diffraction and aberrations limit the maximum spatial frequency at some local region of the image to a cut-off value of f cy/°. A system which optimally samples this region of the image is required by SHANNON's sampling theorem (SHANNON and WEAVER, 1949) to have a minimum angular sampling interval $\Delta\phi = 1/2f$ if its matrix is square, although a hexagonal matrix, the Quincuncial array for packing orchard trees (Sir THOMAS BROWNE, 1912), is more economical (PETERSON and MIDDLETON, 1962; SNYDER and MILLER, 1977b). If finite sampling apertures are employed rather than points then light capture and sensitivity are increased without detriment to the cut-off frequency up to a limiting angular diameter of 1/f if photon noise is ignored. It follows, in such a system whose aperture area $\pi(1/2f)^2$ is associated with a sampling density $(2f)^2$, that coverage, the average number of apertures—or receptive field centres in the case of ganglion cells—which overlap at a retinal point (CLELAND et al., 1975), should be uniform across the retina at the value of π given by $\pi(1/2f)^2 \cdot (2f)^2$ regardless of sampling density. However, the modulation of the output signal from a sampling aperture decreases as its diameter increases and may become lost in photon noise; SNYDER and MILLER (1977b) thus find for an aperture of uniform sensitivity in square array that the diameter, $\Delta\varrho$, is optimal at $\Delta\varrho = 0.586/f$ for a given cut-off frequency. The aperture sensitivity profile for a ganglion cell receptive field appears to be defined by a Gaussian profile (ENROTH-CUGELL and ROBSON, 1966; WÄSSLE and CREUZFELDT, 1973) for which (SNYDER, 1977) the diameter, $\Delta\varrho_G$ defined as 2× the diameter at 50% sensitivity, is given by $\Delta\varrho_G =$

0.75/f; whence/coverage may be derived as $0.56\,\pi$ regardless of sampling density but dependant upon the form of the sensitivity profile of the aperture and the nature of the sampling array. Application of the result is not straightforward. Is the peripheral sampling frequency matched to the cut-off frequency of the image as the theory requires? Does the ganglion cell density of the class involved in resolution relate to acuity according to the requirements of the sampling theorem? Are *on* and *off* cells to be treated separately or as one system? Coverage values are available for the brisk transient class of the cat but the properties of these cells do not appear to be suited to resolution tasks and are not explicitly treated by the theory in the above form. The uniform coverage across the cat retina of 4–6 for the brisk transient class (CLELAND et al., 1975) thus remains in tantalising agreement with both the prediction of constancy and the value required if *on* and *off* systems were separately treated. WÄSSLE and PEICHL (personal communication) have obtained a similar value of 3–4 for cat horizontal cell coverage. The high coverage value of 30 obtained by FISCHER (1973) for the ganglion cell population of the cat retina treated as a whole is large because that population encompasses several classes of receptive field. Most of these classes cannot be incorporated into the above theoretical treatment at present because of the complex nature of their aperture sensitivity profiles. The uniformity of the whole population coverage, however, indicates the general applicability of an inverse relationship between receptive field diameter and sampling density and thus suggests that a theoretical treatment similar to that above may be applicable.

An interesting formalization of these factors for a preliminary model retina has been put forward by SNYDER et al. (1977), who describe the information capacity of a local retinal region as the product of the number of discriminable points with the natural logarithm of the number of discriminable intensity levels. Consideration of sampling aperture, sampling density, quantum capture, and noise within the system establishes that the "number of pictures" is optimal at only one intensity of illumination for a given sampling density with optimal sampling apertures. It follows that all regions of a uniform retina, whether nocturnal or diurnal, have their optimal information capacity at the same level of illumination. If the habits of the species confine it to purely nocturnal or diurnal conditions of illumination, then the illumination levels it encounters would vary little more than 1 log unit, and such a retina would be very efficient. The gradient of sampling density to be found in the retinas of arrhythmic, crepuscular, and auroral species conversely provides retinal regions operating optimally at the differing illumination intensities at which these species are active. It could be argued that the circumscribed area in such forms results from the need for a gradient of sampling density to generate retinal areas optimised for differing levels of illumination. This seems unlikely when the form of the gradients is so obviously adapted to features other than the distribution of light intensity across the visual field. The range of optimal illuminations for such a retina thus appears more probably an outcome of the presence of the ganglion-cell density gradient rather than its primary cause. Similar theoretical treatment of the duplex retina with its *superposed* nocturnal and diurnal systems is a more complex matter for which the necessary information is not yet available. The model has provided some notable insights into the design of compound eyes (SNYDER et al., 1977).

2. The Fovea

The fovea is present at the center of the area retinae of many species of fish, reptile, bird, and all simians (WALLS, 1942; ROCHON-DUVIGNEAUD, 1943; DUKE-ELDER, 1958). In the majority of forms the cones—in tarsius the rods—of the fovea have more elongated outer segments than in the remaining retina, so that the outer limiting membrane may be displaced vitread to form what is described as a *fovea externa*. The long, narrow shape of the central cones is concluded by MILLER and SNYDER (1973) to be more effective in light retention than that of peripheral cones.

The *fovea interna* consists of a localized thinning of the retina accompanied by displacement of ganglion cells to the surrounding perifoveal region as well as reduction in, or complete elimination of, the inner nuclear layer. The fovea may be a concave depression with a relatively flat bottom, concaviclivate, or a narrow but deep pit with convex walls, convexiclivate. In the most extreme convexiclivate fovea the outer nuclear layer may be thinned but more commonly its thickness increases.

CHIEVITZ (1889, 1891) and ZURN (1902) failed detect a fovea interna in a wide variety of subprimate mammals, including mouse, squirrel, hare, shrew, hedgehog, sheep, goat, ox, deer, pig, polecat, dog, and cat. ZURN (1902) described a fovea externa in the cat because of retinal thinning. STONE (1965) reported a 10% reduction in the outer nuclear layer thickness near the area and two layers of ganglion cells instead of the one characteristic at the periphery. BRÜCKNER (1961a) recently claimed a fovea externa to be present in several feline and canid retinas including tiger, puma, panther, lion, leopard, cheetah, wolf and one cat but not in the jaguar, lynx, two cats, and four dogs. However, examination of the alleged cat fovea reveals a depression accompanied by massive reduction of the outer nuclear layer, which is very characteristic of feline central retinal degeneration as described and illustrated by BELLHORN and FISCHER (1970), and BELLHORN et al. (1974); the opposite of what is commonly found in a concaviclivate retina. In all of the other species, except the tiger, the outer nuclear layer is also somewhat reduced, which suggests a pathologic process rather than a fovea.

The function of the fovea pit is a long-standing problem. WALLS (1937) argued on the basis of the refractive-index difference between retina and vitreous, which was reported by VALENTINE (1879b), that the convexiclivate pit of birds and reptiles magnifies the central image and thus aids resolution. Quantitative analysis by PUMPHREY (1948a) revealed that such a fovea would reduce acuity rather than increase it at the foveal center, but at the same time it would induce asymmetry into an off-axis symmetrical image and aid in alignment of the visual axis during tracking. Recently SNYDER and MILLER (1977) have argued that the photoreceptor matrix of some birds is too coarse to account for their claimed behavioural acuity. They suggest that the concave bottom of the convexiclivate fovea, rather than its sides (WALLS, 1937) acts as the negative component of a telephoto lens and provides magnification of a limited part of the local image. The flatter temporal foveae of birds and simians could not function in the manner of the convexiclivate fovea and, according to PUMPHREY (1948a), cannot have much refractive significance. WALLS (1942) regarded the concaviclivate as poorly devel-

oped or degenerate relative to the convexiclivate fovea, but it would now appear to be functionally different.

WOLFF (1940) argued that the retinal layers are displaced at the fovea in order to allow direct access of light to the receptors without reduction of image quality by scattering in overlying tissue; the disadvantage of an inverted retina is thus offset. WEALE(1966) rejected this explanation because the depolarized nonspecularly reflected component of the fundus reflex, which arises during polarized illumination, is similar in proportion from foveal and perifoveal retina, thus indicating that scatter is not introduced by the thickening of the inner nuclear and ganglion cell layers. Instead, WEALE (1966) suggests that blood vessels cannot be tolerated in a high-resolution *area* because of a deleterious influence on image quality, so that the majority of the retinal tissue must be shifted to a region of more adequate nutrient supply. The outer nuclear and bacillary layers are adequately supplied by the choroidal circulation (POLYAK, 1957). An apparent conflict with this theory occurred in *Aotes* retina, where a vessel-free central area was reported to be present in the absence of a fovea, but the problem was resolved when DE OLIVERA and RIPPS (1968) were able to demonstrate the presence of central vessels in this species in contrast to the situation in the rhesus monkey fovea.

It is only necessary, however, to consider the extreme convexiclivate foveae, which are found in the bird retina in spite of the total absence of retinal vasculature, to realise that WEALE'S emphasis on overlying blood vessels rather than neural tissue as the prime factor leading to the formation of the fovea is not adequate in its generality. It is possible that interpretation of the origin of the reflected depolarized light component is in some way inadequate; little is known of its site of origin, and difficulty with it has already been encountered in the interpretation of retinoscopy.

A direct attempt to assess the influence of the inner retinal layers on image quality at the photoreceptor plane has been made by OHZU et al. (1972). In human retinas already showing some signs of deterioration, although very swiftly prepared, the foveal MTF is superior to that of the perifoveal region. The deterioration in quality of image after isolation appears to arise at the inner layers of the retina. The fresh human peripheral retina was not examined, but the MTF of 11-minute-old fovea was superior to fresh rat retina, so that OHZU et al. (1972) suspected that the inner retinal layers were to some extent detrimental to image quality in even fresh human retina. If this is confirmed, their reduction in thickness at the fovea would, contrary to the conclusion of WEALE (1966), be an asset.

If the foveal ganglion cells of man overlay their photoreceptors of origin, then they would require a local density of some 160000/mm^2 and some 30 layers, compared with the maximum of six actually found in the perifoveal region. If retinal scattering is such as to require the foveal tissue to be *thinner* than elsewhere in the retina, then the displacement of this *potential* ganglion-cell accumulation to the perifoveal region must effect an enormous improvement in the local MTF of the area. In a few species, *Lemur catta* and *Indri indri* (ROHEN and CASTENHOLTZ, 1967), the area is actually dome-shaped, as this hypothetical structure would be in man, and is suggested by WALLS (1942) as inevitably effecting some reduction of image size by refraction.

3. Macular, Central and Peripheral Vision

The phrase "macular vision" is often employed to describe central vision in man, but its common extension to vision mediated by the area retinae in the great preponderance of species which lack a macula lutea is unjustified. In fact, the term is probably best avoided altogether, because its use by some authors, e.g., ELLIOT SMITH (1928), has extensive theoretical implications which survive in the backwaters of the literature although insupportable on the basis of current comparative visual physiology. For ELLIOT SMITH, macular vision was the climax of evolutionary development, *the New Vision*, qualitatively different from anything developed in the subprimates. He regarded frontal eyes, conjugate eye movements, and optic fiber decussation as necessary precursors to the development of true macular vision. Once present, the macula leads during evolution to the

> progressive transformation of the brain and eventually to the making of the human mind

ELLIOT SMITH,, 1930). High resolution vision, colour vision, and stereoscopic vision combined with a sophisticated hand lead to the mastery of space. Even the enlargement of the brain arises from the presence of a macula.

DETWILER (1943) criticized these views and pointed out that the anatomic basis of ELLIOT SMITH'S"true macular vision" appears simply to be the fovea and its associated area. However, in many vertebrate species the fovea has developed in the absence of frontal eyes or hemidecussation, and in some birds it is even unrelated to binocular vision, because it deals with the lateral field (WALLS, 1942; DUKE-ELDER, 1958). In such forms there is no trend towards the development of primate-like features, and encephalisation is no greater than in related species with nonfoveate retinas. The evolutionary sequence envisaged by ELLIOT SMITH (1930) as leading to the development of macular vision is thus not a *necessary* chain of events.

ELLIOT SMITH (1930) and many recent workers wrote of the fovea and its area as if it represented an evolutionary functional discontinuity relative to an area retinae lacking the fovea. There is evidence which suggests that the foveal outflow of the macaque retina, unlike the projection of an area in other species, does not reach the superior colliculus (HENDRICKSON et al., 1970); WILSON and TOYNE, 1970; BUNT et al., 1975), but, in general, the known properties of a concaviclivate fovea with an area differ only qualitatively from an nonfoveate area retinae; the convexiclivate fovea may have quite different properties. Features such as high resolution, colour, and stereoscopic vision, which are attributed by ELLIOT SMITH (1928, 1930) to foveate macular vision, are certainly well developed when a fovea is present but are demonstrable in species with only an area retinae.

The pure-cone, rod-free, central zone of the human macula is the basis of high photopic resolution, but vision in this region is qualitatively distinguished from that of the peripheral retina by its scotopic blindness. The high acuity of the area retinae, whether equipped with a fovea or not, again ensures its qualitative differentiation from the periphery because of its use as the image target for the fixation reflex of man and cat (DREHER and ZERNICKI, 1969) and as the region about which directed saccades maintain image centering during fixation (DITCHBORN, 1973). These features, in conjunction with the differentiated appearance of the human mac-

ular region, have led to a general tendency to treat central vision as if it is qualitatively, rather than quantitatively, different from peripheral vision in all species. In the majority of mammals, however, the central area is duplex (Fig. 18), so that the discontinuity of the human pure-cone macular region is absent and the common organization of central and peripheral retina more apparent; it is possible that the photopic and scotopic acuities in the area of such eyes could be very similar, provided that quantum limitations are not involved, and there is no question of a diurnal or nocturnal physiologic scotoma. Even for man the emphasis on the differences between central and peripheral vision is difficult to justify, because most retinal properties such as rod/cone and receptor/ganglion cell ratios, visual acuity, and colour vision, as well as higher level functions like stereoscopic vision and pattern recognition, change in uniform fashion along a centroperipheral gradient over much of which no discontinuity is apparent.

The attention-attracting power of peripheral moving stimuli has often been interpreted as signifying a lower threshold in that region of field and employed to differentiate central and peripheral vision on a qualitative basis:

> Laterally there are two monocular visual fields, each selectively sensitive to change or motion.

(TREVARTHEN, 1968). Measurement of the velocity at which slowly displaced stimuli are just perceived as moving does not support this view, because the *central* movement threshold is found to be much lower than the peripheral (AUBERT, 1886, 1887; RUPPERT, 1908; LICHTENSTEIN, 1963), and the threshold gradient follows a smooth curve as a function of eccentricity. However, the *highest velocity* at which movement is detectable *is* greater for the peripheral than for central field (BHATIA, 1975) but, again, no qualitative distinction is apparent. It remains possible that the subjective impression of qualitatively distinct salience for peripheral, rather than central, moving stimuli reflects some underlying organizational discontinuity between the two regions. The motion sensitivity of the cat Y-cell, or brisk-transient receptive fields, has led to the suggestion that similar cells underly the peripheral motion salience of man (e.g., NELSON, 1974). The implied and ill-defined qualitative difference between central and peripheral motion sensitivity is suggested to be paralleled by the alleged absence of such brisk-transient receptive fields, α-cells, from the cat area centralis (FUKUDA and STONE, 1974), and by their high peripheral percentage. Such suggestions are premature; a more exhaustive investigation of α-cell distribution (WÄSSLE et al., 1975) has indicated, by contrast, that the ratio of α-cells to the total ganglion-cell population is uniform throughout the retina and provides no support for the qualitative differentiation of central and peripheral vision.

III. The Ganglion Cell Layer

The radial organisation of the retina from the photoreceptors to the ganglion cell layer ensures that, away from a fovea, the perikarya of the neural elements overlay the region of the retinal image dealt with by their receptive fields. The local ganglion-cell density thus establishes the maximum number of independent

optic nerve fiber pathways passing to the brain from unit area of retina, or solid angle of field, so that the form of the retinal ganglion-cell distribution determines the retinal sampling distribution over the uniocular field and the available input for more central regions of the nervous system.

At subsequent stages in the visual pathways it is found that the topographic mapping of the visual field onto various regions of the CNS is such that retinal regions of high ganglion-cell density obtain proportionately greater representation than those of low density. The topography of central stations on the visual pathway is thus *usually* determined by the effective peripheral innervation density as for other sensory modalities (WHITTERIDGE, 1973).

The retinal ganglion-cell density map therefore provides not only a rough guide to the variation in quality of vision with retinal eccentricity (although with caveats detailed later) but is also representative of the central neural provision for each region of the uniocular field. A knowledge of the relative positioning of the two eyes and of the retinal ganglion-cell distribution thus provides an easily accessible basis for investigating adaptations in the use of visual space which are peculiar to a given life style and characteristic of a species entire visual system.

Just as the total photoreceptor population determines the potential maximum number of independent data available to the retina, so does the retinal ganglion-cell population set a limit on the proportion of this information which is passed on to the central nervous system via that "bottleneck" on information flow in the visual system, the optic nerve (RUSHTON, 1962). Before dealing with the topography of the ganglion cell layer, it is worth briefly considering its total channel capacity as indicated by the optic nerve fiber population.

1. Channel Capacity of the Retinal Ganglion Cell Layer as Determined from the Optic Nerve Count

The optic nerve contains the axons of the retinal ganglion cells which are passing to the brain and a population of efferent fibers on their way to the retina. In the pigeon such efferent fibers amount to only about 1% of the total fiber population of the nerve (COWAN and POWELL, 1963), and similar proportions have been reported by BROOKE et al. (1965) in monkey and cat. The rabbit is also said to possess efferent optic nerve fibers (CRAGG, 1962), but in no mammalian species has the proportion been described as over 1% of the total nerve fiber population and in fact the presence of efferent fibers has been questioned for the cat by BRINDLEY and HAMASAKI (1966). It is acceptable therefore to employ the optic nerve fiber total count as an index of the total retinal ganglion-cell population of a given species.

A great range in the magnitude of the total optic nerve fiber population was documented among vertebrate species by the classic light microscopic studies of BRUESCH and AREY (1942), but so far no teleologic basis has been put forward to explain the distribution of high and low counts; the optic nerve fiber population did not appear to correlate with eye size, laterality of eye position, or primary adaptation to photopic or scotopic vision.

At present, however, it appears that all of the earlier work requires reexamination; MATURANA (1959) has demonstrated that light microscopy underestimates

the anuran optic nerve fiber population by a factor of thirty because of its failure to resolve a large population of unmyelinated nerve fibers. Subsequently it was noted that even in the rat optic nerve, where all the fibers are myelinated, the light microscope fails to reveal 60% of the fiber population identifiable by means of the electron microscope (FORRESTER and PETERS, 1967). Similarly, some 50% of pigeon myelinated fibers, and unmyelinated fibers amounting to 30% of the total count, remained unresolved by light microscopy (BINGGELI and PAULE, 1969).

It is surprising to find that, in spite of these results, several recent investigators of duck (O'FLAHERTY, 1971) and teleost (TAPP, 1973) have employed the electron microscope to determine fiber-diameter spectra but depend upon light microscopy for their total counts. It is commonly assumed that light microscopy will resolve fibers of at least 0.6 μm diameter (FORRESTER and PETERS, 1967) or less under phase contrast, 0.25 μm (POTTS et al., 1972), but resolution may be drastically reduced by slight deviations from optimal conditions. A recent reexamination of the cat optic nerve by electron microscopy (HUGHES and WÄSSLE, 1975) indicates the light microscopic study of DONOVAN (1967) to have recorded only 6% of fibers 1 μm diameter and 75% of 2 μm fibers; it is to be noted, however, that BISHOP and CLARE (1955) employed light microscopy and obtained a fiber-diameter spectrum identical to that of the electron microscope study. Whatever the reasons for the poor performance of light microscopy under certain conditions, it obviously must not be employed without electron microscopic controls. The absence of such controls means that reservations must be entertained about the recent, and otherwise model, attempt to completely enumerate the axons of the human optic nerve (POTTS et al., 1972). by phase microscopy of thin sections. The resulting total of 1.1–1.3 million fibers was almost identical to that of BRUESCH and AREY (1942) instead of showing an increase of up to 50% such as has occurred upon electron microscopic reexamination of other species with larger modal-axon diameters.

Total fibre counts based upon electron microscope examination are available for only a few mammals: rat (FORRESTER and PETERS, 1967; HUGHES, 1977), 118000; cat (HUGHES and WÄSSLE, 1976), 193000; rabbit (VANEY and HUGHES, 1976), 395000; hamster (TIAO and BLAKEMORE, 1976) 119000; the consideration of so few species can be of little value; there is more profit in comparative examination of the local speculations for resolution in the area retinae and fovea and the overall retinal ganglion-cell distribution.

2. Quantitative Mammalian Retinal Ganglion-Cell Topography

Quantitative maps of ganglion-cell density distributions have been constructed from counts along radial retinal sections of several mammalian species including rat (LASHLEY, 1932), rabbit (SENEVIRATNE, 1963), man (VAN BUREN, 1963), suiformes (LUCK, 1965), baboon (WHITTERIDGE, 1965), and pinnipeds (LANDAU and DAWSON, 1970), but the method is subject to error (e.g., ABERCROMBIE, 1946), and more satisfactory results are obtained by counting ganglion cells in flat mounts of the entire retina (STONE, 1965).

The definitive criterion for the identification of a neurone of the retinal ganglion-cell layer as a retinal ganglion cell is that it sends an axon into the optic

Table 4

	Cat	Rabbit	Pigeon
A. Optic nerve count	193000	397000	4200000
B. Ganglion cell-layer neurone count	190000–260000	450000–520000	2380000
Ratio of A/B	0.98–0.75	0.88–0.75	0.57

Sources of data: cat, HUGHES and WÄSSLE (1976), WÄSSLE et al. (1975), HUGHES (1975a); rabbit, VANEY and HUGHES (1976); pigeon, BINGGELI and PAULE (1969).

nerve. Unfortunately, neither the dendritic morphology nor the axon are visible in Nissl-stained flat mounts, and the cells of the retinal ganglion-cell layer must be classified by the appearance of their perikarya alone.

The presence of Nissl substance enables the differentiation of neurones of the ganglion-cell layer from the glia and vascular elements (STONE, 1965; HUGHES, 1975a). It is, however, difficult to asses the influence of displaced amacrine cells (CAJAL, 1892; GALLEGO, 1971) on the count. If such cells show Nissl substance, they will be miscounted as neurones, but if stained like cells of the inner nuclear layer they could be classified as glia. The total fiber count of the optic nerve may be compared with the integrated ganglion-cell count from the map as a test of the criteria (HUGHES, 1975a), but for most species the necessary information is not available for such a control. The only results based upon integrated retinal whole-mount density maps and electron microscope nerve fiber total counts are contained in Table 4. Recently, TIAO and BLAKEMORE (1976) reported some 119000 optic nerve fibres and 114000 ganglion cells in hamster retina, a ratio of 1.04. VANEY (1977) has employed the advantageous arrangement of the rabbit retinal fibre bundles to count the fibre efflux from a specific retinal area and thus establish the local ganglion cell count. His streak ganglion cell densities are within 80% and peripheral densities within 60–70% of previous presumed-ganglion-cell maps (VANEY and HUGHES, 1976). A substantial proportion of the difference is accounted for by neurones which do not project to the optic nerve.

Earlier results like those of AREY and GORE (1942), who obtained a ratio of 0.94 of optic nerve fiber to ganglion cells in the dog, require reexamination with modern methods before acceptance. The above ratios, ignoring miscounted glia, clearly indicate the possibility of a much smaller proportion of internuncial retinal neurones in the mammals than in the birds, which is in keeping with known retinal histology (CAJAL, 1955). That cells with the appearance of neurones remain after optic-nerve section has been reported for the cat (LEINFELDER, 1938) and rat (EAYRS, 1952) but denied for rabbit (JAMES, 1933) and kitten (STONE, 1965). Again, modern criteria must be applied for the reconsideration of these results. Although FUKUDA (1977) has claimed agreement between published rat optic nerve counts (118000, FORRESTER and PETERS, 1967) and his integrated ganglion cell density map (115000), it has been pointed out by HUGHES (1977d) that a more satisfactory integration of his map indicates the presence of 145000 ganglion cells. HUGHES' unpublished neurone count for the rat indicates between 125000 and 190000 cells in contrast to 120000 optic nerve fibre in an animal of the same strain (HUGHES, 1977d). It remains to be seen whether the excess cells are really neurones or mis-classified glia. For the present, the maps subsequently

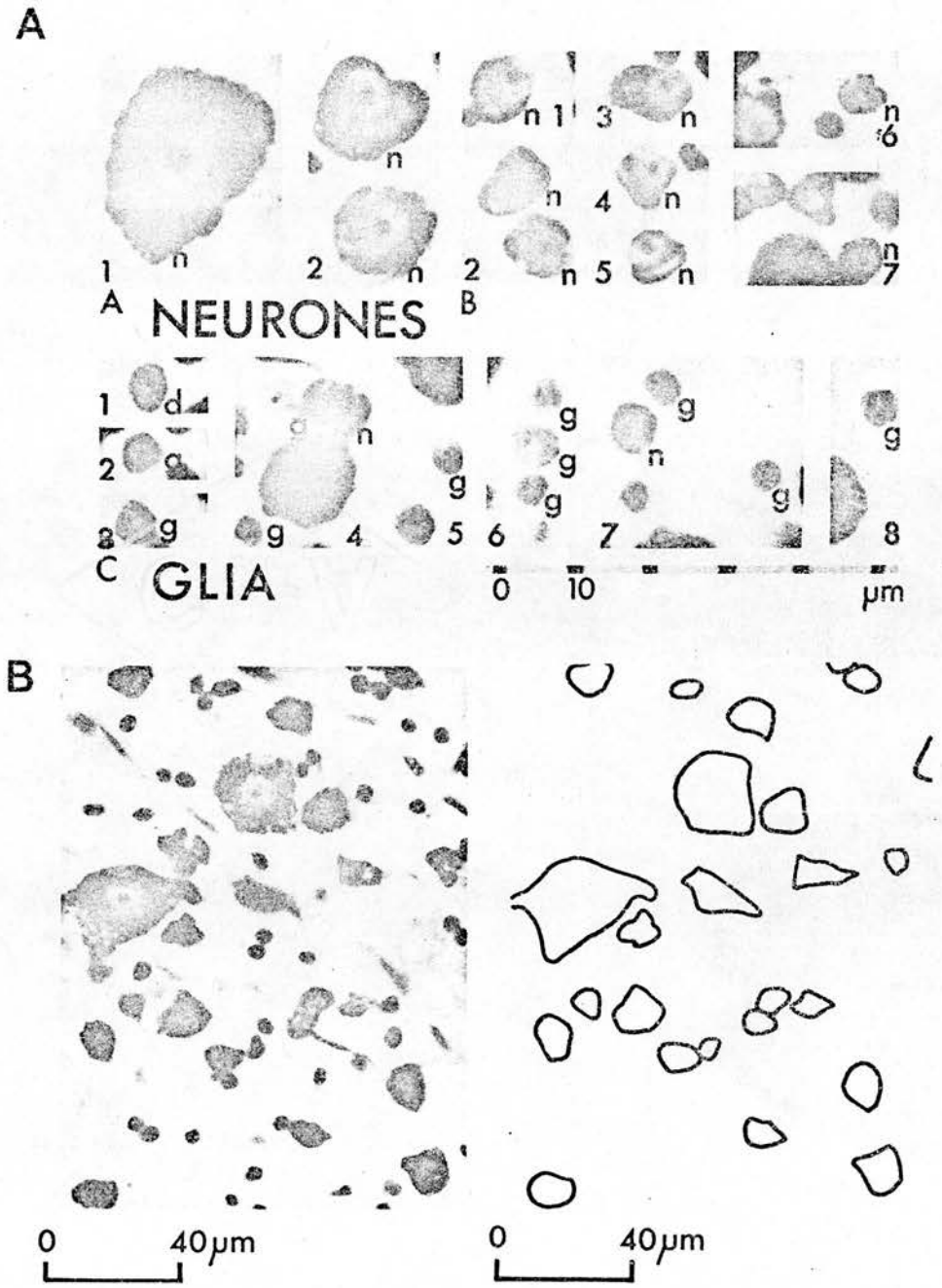

Fig. 19. Criterion examples of ganglion cells in retina of cat: *A*, neurones of retinal ganglion-cell layer, *n*, identified by their Nissl staining. Doubtful cell, *d*, and glial cells of the same layer, *g*. The neurones are presumed ganglion cells; *B*, a photograph of an area of cat visual streak accompanied by the outlines of presumed ganglion cells which have been identified under oil immersion. (After HUGHES, 1975a)

presented must be regarded as provisional and as showing the distribution of *presumed ganglion cells*.

Some criterion examples of retinal ganglion cells and glia from the cat retina (HUGHES, 1975a) are presented in Fig. 19a, and a region of the cat visual streak shown in Fig. 19b with a key to the identified ganglion cells. The general appearance of the cell types is similar to those of the cat in the majority of mammalian species examined.

The recent development of methods which enable the retrograde transport of various identifiable materials, such as cobaltous chloride (LINCOLN and MASON, 1974) or horseradish peroxidase (HRP; LA VAIL and LA VAIL, 1974), from the axon terminal up to its perikaryon promises more certain identification of the retinal ganglion cells, but difficulties remain. BLUNT et al. (1974) have reported on the passage of HRP along the optic nerve of the rat but find that the enzyme does not enter a substantial population of small cells in the retinal ganglion-cell layer. These cells look like small neurones but may be interneurones, nontransporting ganglion cells, or ganglion cells which project to sites other than those injected.

Quantitative ganglion-cell distribution maps based upon flat-mount preparations are now available in the literature for several mammalian species: cat (STONE, 1965; HUGHES, 1975a), rabbit (HUGHES, 1971), goat (HUGHES and WHITTERIDGE, 1973), and plains and tree kangaroos (HUGHES, 1975a), owl monkey (WEBB and KAAS, 1976), rat (FUKUDA, 1977), hamster (TIAO and BLAKEMORE, 1976). From these and the author's unpublished material it is possible to select a representative series of mammalian retinas such as is illustrated in Fig. 20.

No mammal so far investigated has been found to lack both streak and an area. Among the species which lack a visual streak, the characteristic feature of the isodensity contours is the relatively high degree of radial symmetry. Three classes of such distribution may be distinguished:

a) Low Ganglion-Cell Density with Little Centroperipheral Density Gradient. This is typical of small nocturnal inhabitants of the undergrowth such as the guinea pig (Fig. 20a), mouse, weasel, etc. In a more arrhythmic species, such as the rat, the area may be better defined (Fig. 20b). It is not, however, true that

> The mouse and rat have nothing that can be recognised as indicating an area where vision is anything but indifferent!

(PRINCE, 1956). All encountered nocturnal forms do have a region of higher density about the fixation axis. In the rat (HUGHES, 1977c), and probably other nocturnal forms, this region is accompanied by an increased cone density in the subadjacent receptor layer.

b) High Ganglion-Cell Density with Little Centroperipheral Density Gradient. Such a distribution is characteristic of the predominantly diurnal retina such as is found in the tree shrew or squirrel (Fig. 20c). The ganglion-cell density changes no more than three- or fourfold from the area to the periphery, the condition described as "universal macularity" by ROCHON-DUVIGNEAUD (1943).

c) Steep Centroperipheral Density Gradient. Such a distribution reveals a precisely localised visual pole and is to be found in man (Fig. 20e) (VAN BUREN, 1963), baboon (WHITTERIDGE, (1965), and other primates; although the area retinae is associated with a fovea in both of these species, this is not inevitable.

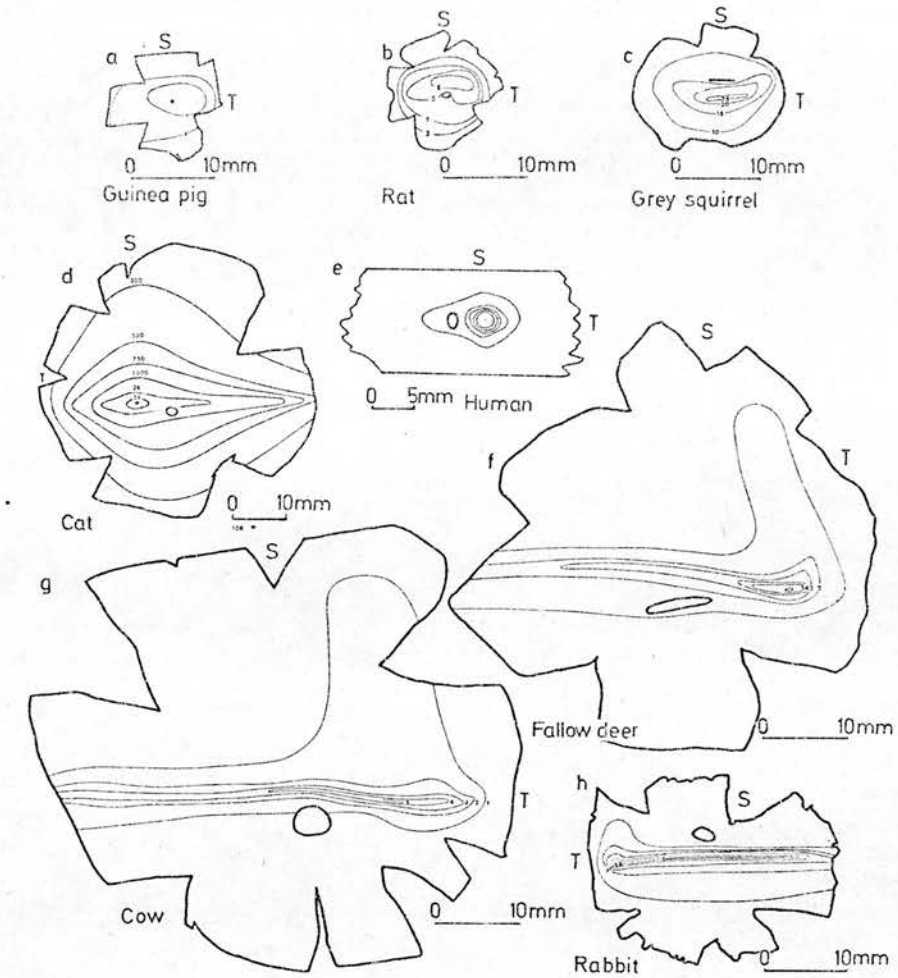

Fig. 20. Presumed ganglion-cell density distribution maps derived from counts made on the Nissl-stained retinas of various mammalian species. The teleologic basis for the differing forms of these maps is discussed in the text. The isocount lines indicate changes of density in steps of 1000 ganglion cell/mm² or multiples thereof; the human map, after VAN BUREN (1963), is an exception in that it indicates the number of layers of ganglion cells between one and five. All species so far examined have revealed some degree of area differentiation

The construction of ganglion-cell distribution maps has revealed that a large number of mammals possess mixed retinas in which a visual streak is combined with an area of the type (c) above.

d) Central or Temporal Area Superposed on a Visual Streak. The best investigated retina containing a relatively central area in association with a visual streak is that of the cat (Fig. 20d), but a similar arrangement is to be found in most carnivores, including the dog, mongoose, and polecat. No different in principle is the temporal area found associated with the visual streak in the more lateral-eyed herbivorous species, such as the fallow deer (Fig. 20f), sheep, goat, horse, or red

kangaroo. The more temporal situation of the area than in carnivores simply enables the visual axis to remain in the parasagittal plane in spite of the lateral position of the eyes. The relative quality of the area and streak differs between species; the cow is an extreme member of this group, with a very poorly defined area (Fig. 20g) and almost qualifies for the final class of distribution.

e) Visual Streak Unassociated with an Area. This distribution is the most extreme deviation from that found in man but is rarely encountered in pure form among the mammals. The rabbit (Fig. 20h) shows it to best effect, but it is also present in the ground squirrel and mongolian gerbil.

Among many of the herbivores there is a conspicuous upward bulge of the lower density isocount contours in a region bridging the decussation line above the visual pole; its upward extension is much greater in the tall species (Fig. 20g) than the short (Fig. 20h). This feature is as distinctive as the area or visual streak in the isocount maps and is subsequently referred to as "the anakatabatic area".

3. Retinal Ganglion-Cell Topography in Nonmammalian Classes

Extensive macroscopic examinations of the nonmammalian vertebrate fundus have been published (CHIEVITZ, 1889, 1891; SLONAKER, 1897; WOOD, 1917; FRANZ, 1934; WALLS, 1942; ROCHON-DUVIGNEAUD, 1943; DUKE-ELDER, 1958), although there are very few quantitative ganglion-cell distribution maps available for this group: frog (JACOBSEN, 1962), pigeon (WHITTERIDGE, 1965; BINGGELI and PAULE, 1969), and the kelp bass (SCHWASSMANN, 1968). No vertebrate species whose retina has been microscopically examined has been found to lack at least the rudiments of an area retinae; the term "amacular fundus" coined by WOOD (1917) is applicable only to the macroscopic appearance of the retina. The fovea is singularly lacking among the mammalian subprimates but common in fish, reptiles, and birds. With the exception of the birds, the circular or oval area retinae is located for forward vision so that its nasal or temporal retinal position is determined by the laterality of the eye position in the head. Among birds, however, macroscopic examination indicates examples of a central area for lateral viewing, two areas (bimacular fundus), or even two areas superposed on a visual streak, the *infulabimacular fundus* (WOOD, 1917), but these organizations require quantitative substantiation. Macroscopic examination also reveals the visual streak to be common among birds (CHIEVITZ, 1889, 1891; SLONAKER, 1897; WOOD, 1917; O'DAY, 1940; DUIJM, 1959); in addition, it is present in certain sharks (FRANZ, 1931) and teleosts (BUTCHER, 1938; ENGSTRÖM, 1963; MUNK, 1970) but not in many other fish (KAHMANN, 1934; TAMURA, 1957; SCHWASSMANN, 1958), anurans (CHIEVITZ, 1889, 1891; SLONAKER, 1897; GAUPP, 1904; JACOBSEN, 1962), chelonians (HESS, 1913; BROWN, 1969), lacertilia (SLONAKER, 1897; KAHMANN, 1936), and crocodilia (CHIEVITZ, 1889, 1891). Unique among the studied vertebrate retinae are those of two cyprinodontid fish (MUNK, 1970) which have a *bi-infular fundus* containing two parallel visual streaks about which more will be said later. In that the common belief that the visual streak is rare among the mammals has been dispelled by quantitative examination of ganglion-cell distribution, so must the results of macroscopic examination on other vertebrates await detailed reexamination before its absence in any species is regarded as established.

IV. Function of the Visual Streak

1. Current Theories

It was clear to the earliest students of the vertebrate area retinae that there is no correlation between phylogenetic status and retinal ganglion-cell topography. The great variety of area shapes also suggests that their form is not simply an outcome of some convenient morphogenic process which is without functional significance. The possibility of a relationship between the life style of a species and the form of its area was raised by CHIEVITZ (1889), but neither he, SLONAKER (1897), nor ZURN (1902) attempted functional interpretation of ganglion-cell topography, and neglect of this topic continues in the classic accounts of retinal reorganisation (FRANZ, 1934; WALLS, 1942; ROCHON-DUVIGNEAUD, 1943; DUKE-ELDER, 1958).

The elongated visual streak was obviously understood by JOHNSON (1901) to be of protective value; thus he refers to the ungulates as species which

> graze in the proper sense of the word. They poke their heads down into the long sharp grass, while they are notoriously those which have most need of being on the alert for Carnivores, their natural enemies,

and couples the need for panoramic vision with an extended area:

> those animals which have a widely extended sensitive area and need to see all round them.

The idea is more explicit in VINCENT (1912), who suggests that the central area

> seems to be larger in those animals where the divergence of the optic axes is great and when combined with nearly spherical lenses and large corneas it gives the animal a wide range of vision.
>
> The ability to see on all sides gives the animal greater security from enemies ...

A comparative study of retinal organisation among the Suidae led LUCK (1965) to suggest that the visual streak provides more than panoramic vision. The prominent streak of the wart hog implies that its organisation

> accords well with its habitat and habits. It is the eye of an animal living by day in the open country and in one plane. Food and foe alike come to it from the ground and this horizontal plane of interest is reflected by the retinal horizontal streak area.

The absence of the streak in the bush pig retina is suggested by LUCK (1965) to result from the equal importance of the vertical and horizontal planes as a source of danger in its natural habitat. The linear area centralis of the turtle led BROWN (1969) to a similar conclusion, that in an animal

> which never rises far above water or ground, most visual stimuli which are important must come from the region of the horizon. Hence the linear and horizontal area centralis appears to be a highly functional specialisation for an animal living close to the earth's surface!

This suggestion is in striking contrast to the description of the bird visual streak as employed in navigation during flight at considerable height above the ground (PENNYCUICK, 1960; MATHEWS, 1968)! But the ad hoc nature of this hypothesis is indicated by the absence of a streak in the pigeon (BINGGELI and PAULE, 1969), which is a skilled navigator, and other migrating birds (DUIJM,

1959). Other theories are equally unsubstantiated. Thus, for PUMPHREY (1948b) the visual streak in birds of the sea, desert, and open spaces

> suggests a device for accurately fixating the horizon as a datum to which other objects in the visual field can be referred.

Why such a reference should be needed when absent from forest-dwelling species, which appear upon macroscopic examination to possess only circular areas' remains unexplained. In any event, it remains to be demonstrated that the bird streak is specifically adapted for use during flight. Its presence in the albatross (O'DAY, 1940) suggests, in view of the long diurnal periods spent on the wing, that the streak plays some role in flight. According to WOOD (1917) the streak is common in ground feeding birds and

> probably enables the bird to widen the limits of his field of distinct vision (especially while feeding) without being obliged to move the whole head.

At least such a hypothesis is applicable to the other vertebrate classes containing members with visual streaks.

2. Counter-Examples to the Current Hypotheses: The "Terrain" Theory

The availability to the author of retinal ganglion-cell distributions for nearly 100 mammalian species makes it possible to assess the general applicability of these hypotheses more rigorously. The common extension of JOHNSON's (1901) theory that the streak is correlated with lateral eyes, a wide panoramic field, grazing habits, and subjection to predation is well substantiated by its presence in the rabbit, hare, and ox as well as deer, sheep, horse, and plains kangaroo (HUGHES, 1975b) (Fig. 21a) in association with an area temporalis.

Unfortunately for the attractive simplicity of this view, there are several counter-examples available. The presence of the visual streak in the crocodile (CHIEVITZ, 1889) reveals that this distribution may occur in predatory as well as preyed-upon species. Of course, the crocodile is lateral eyed, but that the streak is not confined to *lateral eyed* predators has been recorded in the literature since Slonaker's report of a bandlike area in the relatively frontal-eyed fox and cat (1897). An "arm of high ganglion-cell density" in the cat distribution was confirmed by STONE (1965) and subsequently shown to be prominent enough to merit description as a visual streak (HUGHES, 1975a). Various stages of streak development are present in the more frontal-eyed carnivores, such as the dog (Fig. 21b) (collie, greyhound, beagle, dingo) as well as the fox, polecat, and mongoose. The observation (WHITTERIDGE, personal communication) that the blood vessels of the cheetah fundus (JOHNSON, 1901) suggest the presence of a streak led to the discovery of a well-developed example of such a distribution (Fig. 21c) in conjunction with a circular area. In this instance, we find a frontal-eyed predator with nearly parallel optic axes to be in possession of a very pronounced visual streak. It thus does not follow that a bandlike retinal area

> invariably accompanies a particular position of the eyes.

(PRINCE, 1956), nor is it uniquely associated with either prey or predatory species.

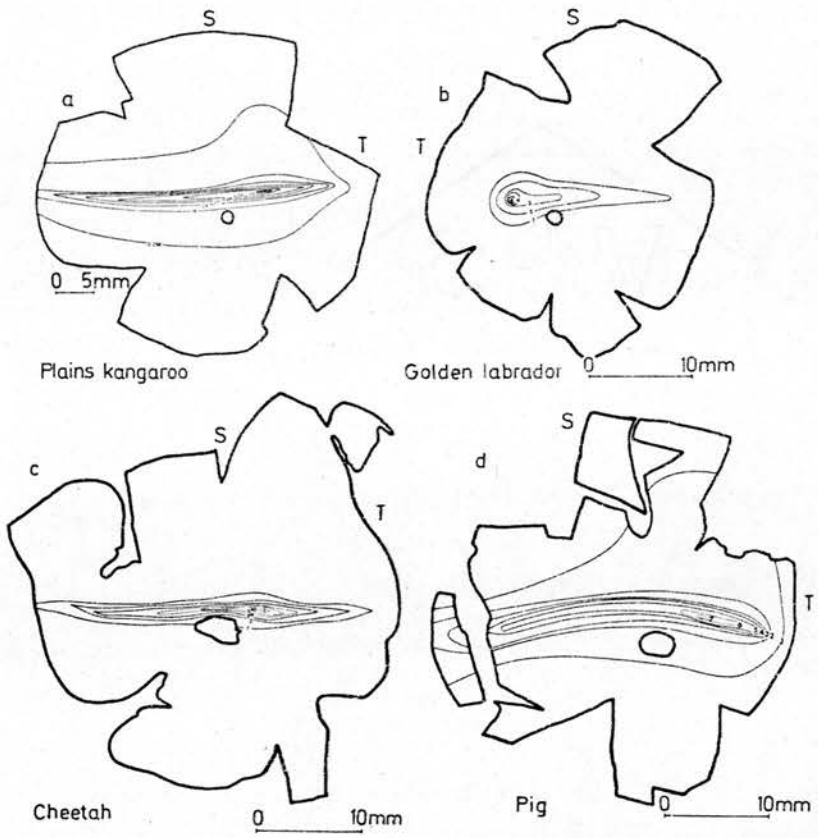

Fig. 21. More retinal ganglion-cell distribution maps which are discussed in text. Conventions same as for Figure 20. Note well-developed visual streak and area centralis in retina of the frontal-eyed cheetah

Of the original conglomerate hypothesis only the association. betweeen the presence of a visual streak and open-country habitat (LUCK, 1965; WHITTERIDGE, 1973) has not so far been contested. It is striking that the best-developed visual streaks among the investigated carnivores are those of the cheetah, which depends upon open country for its hunting, and the greyhound, which is a specialized desert hunting dog (FIENNES and FIENNES, 1968). Numerous other forms substantiate this correlation, including the sea and desert birds (PUMPHREY, 1948), open plains and desert-living mammals, such as the wart hog (LUCK, 1965), ground squirrel, mongolian gerbil, antechinomys and its placental counterpart, notomys (HUGHES, unpublished). In keeping with the association between the visual streak and an open-country habitat is the presence of this organ in bottom-feeding sharks (MUNK, 1970) and the mudskipper of the intertidal flats (MUNK, 1970). However, even this generalizations has counter-examples. Thus, the visual streak of the pig (Fig. 21 d) is as well developed as that of the ox, and yet the former species has been a forest dweller since its origin in the oligocene (COLBERT, 1967). Again, the grey kangaroo visual streak is as prominent as that of the plains

kangaroo (HUGHES, 1975a), and yet the former is characteristic of wooded country and never enters open grass or shrub-covered plains (FRITH, 1973).

The visual streak is, however, by no means universal even among terrestial animals. It is entirely absent among small nocturnal species of the thick undergrowth, such as the hedgehog, mouse, guinea pig, and to a lesser extent, the rat, whose retinal ganglion-cell population is fairly uniformly distributed across the retina.

Amongst arboreal species, such as the tree shrew, tree kangaroo (HUGHES, 1975a), grey squirrel, squirrel glider, and macaque, it is found that the ganglion-cell distribution is quite radially symmetrical with the projection of its center of symmetry aligned for forward vision.

The conclusion to be reached from these results is that the visual streak is common to terrestial species whose field of view is not completely obscured by nearby vegetation and not simply to those which occupy open country, as suggested by LUCK (1965); the terrain surface is overt in all but the most overgrown woods, above the stream bed to a fish, or above the sea to a flying or floating bird.

3. The Retinal Image of a Stationary Eye Above an Extensive Terrain

The advantage of the visual streak is readily understood from the projective transformation of an extensive terrain into the retinal image. Consider an object as it moves longitudinally along the surface of an extensive plain away from a stationary eye at height, h, whose effective image shell is bisected by the image of the horizon. As the object distance, d, increases, its image passes down the superior retina towards the projection of the horizon line at the equator of the globe. The angular elevation, θ, of the object's image above that of the horizon line may be regarded with little error ($< 7\%$ when d is in excess of $2.5h$) as varying inversely with the object distance:

$$\theta = \arctan h/d \approx h/d \text{ radians}.$$

The image of the terrain from $d = 2.5h$ to infinity is thus packed into a strip of the image shell subtending only 21° of the 90° superior quadrant. Beyond $100h$ the entire terrain is imaged in a strip only 0.6° wide.

The invariant features of this image were first noted by GIBSON (1950):

> An out-of-doors world is one in which the lower portion of the visual field ... is invariably filled by a projection of the terrain. The upper portion of the visual field is usually filled with a projection of the sky. Between the upper and lower portions is the skyline ... always cutting the normal visual field in a horizontal section ... It is little noticed, but on the average and over the ages it must have determined the fundamental pattern of retinal images for all or most terrestial animals.

The majority of terrestial objects and events are thus represented in a horizontal strip of the retinal image, and their detection is most economically ensured by the concentration of ganglion cells in the corresponding region of the retina to form a visual streak. The effective evolution of such a streak requires, however, that the receptors which supply the input to the streak be kept in fixed relation-

ship with the retinal image of the terrain and horizon. The validity of the "terrain" theory thus necessitates that the streak be horizontal under normal conditions and resist displacement when the orientation of the head is changed.

The specific examination of the visual streak's projection into the visual field of the rabbit (HUGHES, 1971), goat (HUGHES and WHITTERIDGE, 1973), and cat (HUGHES, 1976a) indicates that it is indeed horizontal and aligned close to the visual horizon of these animals when they are consicious. Although some authors (SLONAKER, 1897; WOOD, 1917) appear to accept that the streak is oblique in certain birds, it is in fact found to be horizontal (DUIJM, 1959) if the normal head position is taken into account, according to the suggestion of PUMPHREY (1948b). The necessary dynamic reflex maintenance of the horizontal alignment of the visual streak over a wide range of passive head rotation has been demonstrated to exist in turtle (BROWN, 1969), rabbit (HUGHES, 1971), and goat (FORRESTER, 1975) according to the requirements of the above hypothesis.

For arboreal, as for terrestrial, forest species, it is unlikely that obscuration of the terrain is total. The absence of the visual streak among arboreal forms is rather accounted for by the lack of a fixed relationship between the image of the visible terrain and any part of the retina. The situation for a climbing animal which swings or jumps through the branches while viewing the world from different orientations is quite different to that of many birds which fly in relatively constant orientation and with an overt horizon.

So little light penetrates the undergrowth and hedge-rows from dusk to dawn that for the small nocturnal animals

> Vision at a distance is therefore altogether impossible in a dim light

(WALLS, 1942). The distant terrain would thus be invisible even if not obscured and a visual streak of no benefit. It is more puzzling to find that the secondarily terrestrial baboon (WHITTERIDGE, 1965) and man (VAN BUREN, 1963) show only slight horizontal ellipticity of their ganglion-cell isodensity maps in lieu of a visual streak. However, in spite of their terrestrial habits, these species retain a much greater variety of eye and head positions than is encountered in streak-bearing quadrupeds, and it is subsequently suggested that their sampling distribution is adapted to the analysis of the dynamic retinal image.

4. Quantitative Models of the Retinal Ganglion-Cell Topography

It is a commonplace of information theory that a finite-state information channel like the optic nerve attains its maximal information-transmission rate only when its states are maximally uncertain—a condition achieved if they are equiprobable or when the probability of activation of each element is equal. Any statistical nonuniformity or invariance in the information source which is not matched by a corresponding modification of the sampling distribution ensures nonoptimal encoding. It is thus arguable that the sampling distribution should match the distribution of source information when encoding by sampling over an information source like the retinal image.

The accepted concept of the evolutionary adaptation of the retina to the needs of a species implicitly accepts some approach to optimal encoding with respect to

both *habitat* and *life style*. The information source to which the sampling distribution is adapted cannot be regarded as the retinal image of the habitat but only as those components, the *information array*, which are important to the animal in its specific lifestyle. The visual world extends about an animal in all directions, but vulnerability to rapacious birds makes a high-resolution survey of the entire sky necessary for small species although redundant for large forms. Again, although the terrain may be statistically invariant around an animal, the extent and quality of its visual analysis is weighted according to life style by the degree of laterality of the eyes and the retinal provision for the analysis of the lateral field. It thus follows that a comparison between a sampling distribution and the invariant features of the typical retinal image cannot *necessarily* be expected to give immediate insight into its functional significance but, at least, the attempt is worthwhile.

The open-country (LUCK, 1965) and terrain theories of the streak employ the high probability, assessed on the basis of ecologic knowledge, that the retinal image of streak-bearing species will contain an invariant and foreshortened image of an extensive terrain to hypothesise that the distribution is adapted to deal with the ground surface and its contents. A variety of quantitative distributions are compatible with this hypotheses, depending upon the feature to which the sampling array is optimally matched.

Certain cautions are necessary before theoretical treatment. The sampling distribution is discussed as if involved in a *generalized resolution task;* its elements are treated as if functionally equipotential, and the sampling theorem is regarded as determining the resolution obtainable from a region of given sampling density (SHANNON and WEAVER, 1949). It is obvious that the presentation is based upon the assumption of an idealized environment which may be realized in life only as stochastic features of the retinal image. The inadequacies of these assumptions are taken up subsequently, and many of the terms discussed in more detail.

a) Constant Angular Resolution

First consider a visual streak or entire retina across which the sampling rate is uniform. From the sampling theorem we have that the angular resolution, α, achieved by an ideal system varies inversely as the effective sampling rate, $\alpha = 2/r$. Now the angular magnitude, ϕ, of the image of an object with a frontal dimension, w, varies inversely as its distance, d, from the eye according to the law of visual angle,

$$\phi = \arctan w/d \approx w/d \text{ radians } (e < 7\% \text{ if } w/d < 0.4)\,.$$

Setting w equal to the absolute frontal dimension, s, of the minimum separabile, we obtain $\phi = \alpha$ and may write

$$s = 2 \cdot d/r\,.$$

Within such a region of uniform sampling rate, the size of resolvable detail, the minimum separabile, is uniquely correlated with stimulus distance and increases as the stimulus approaches the eye regardless of its path. A visual streak of uniformly elevated sampling rate relative to the peripheral retina, such as is envisaged by MUNK (1970), gains the advantage of an increased resolution for the terrain and its contents. A uniform sampling rate over the entire retina would be suited to a static eye whose homogeneous environment contains information uniformly distributed over all directions or whose distance vision is so limited in extent as to minimize the effects of perspective in the retinal image and render ineffective the subsequently described distribution.

b) Constant Size Resolution in the Local Frontal Plane

It is clear from above that if $r \propto d$, the absolute size of the minimum separabile would remain constant with increasing stimulus distance. This could *not* be easily achieved when images from objects at different distances have no differential distribution across the retina. But consider an eye of which the information array consists of the objects and features of an extensive terrain above which it is set at height, h, with the image of the horizon line coincident with the equator of the globe. Because the terrain and its content at a given distance project to a unique elevation in the image, θ, it is possible for the local sampling rate to be arranged to vary as the distance of the corresponding terrain and thus inversely as its elevation on the superior retina. We may write

$$r = \frac{2 \cdot h}{s} \cdot \frac{1}{\theta}$$

so that the dimension of the minimum separabile remains constant with increasing distance until $r \neq k/\theta$. The possibility of only a finite maximal sampling rate ensures that this must occur for some limiting distance, d_l. A plot of r against θ is thus a truncated rectangular hyperbola for such a retina; the horizontal sampling rate is uniform along the retina at any elevation.

The reduction in angular subtense and decreasing elevation of the images of a uniformly distributed and homogeneous population of objects with increase of their distance from the eye along a flat terrain is described by GIBSON (1950) as a gradient of visual texture in the retinal image. It has been suggested (HUGHES, 1975a) that the sampling profile across the streak is matched to the gradient of visual texture in the image, but difficulty arises with this terminology. Obviously such a gradient exists for any *specific* population of objects, but in the natural image the nearer objects reveal, as do the distant, grades of texture up to the limit of optical resolution, so that the gradient of visual texture is not objectively demonstrable without reference to higher level feature-recognition processes. The more fundamental description of this model is that it eliminates redundancy introduced into the image by the law of visual angle and simultaneously achieves constant size resolution in the local *frontal* plane along an extended flat terrain.

The terrain of the real world is populated with objects of vertical extension which is substantial in relation to the height of the eye. When close to the eye the vertical projection of such stimuli in the retinal image extends over regions of ganglion-cell density not matched to their distance from the eye. However, because the vertical angular subtense of such stimuli in the retinal image decreases in proportion to their distance from the eye, it follows that their images become progressively better confined to a region of ganglion-cell density matched to their distance if they move away along the terrain surface. The sampling profile which achieves constant size resolution is thus most appropriate under circumstances in which the information array consists of the terrain and its contents very distant in terms of h.

Examination of the projection of the visual streak in several species (e.g., rabbit, HUGHES, 1971) indicates that the vertical ganglion-cell profile is fairly symmetrical about the region close to the image of the horizon line. *The high-density region of the streak is thus adapted to the image of the upper field as well as to that of the terrain*, a situation not encompassed in the open-country or terrain theories of the streak but compatible with the constant size resolution or "inversion of the law of visual angle" model. Although less clearly defined, an aerial horizon similar to that of the ground may be regarded as implicit in the inferior retinal image of the sky. If, for instance, the distribution of rapacious birds forms the information array for the eye, then the relatively limited range of their altitude would suffice to stochastically determine its parameters. Qualitative consideration suggests that variation in the vertical sampling rate of the inferior retina according to a rectangular hyperbola or an approximate pragmatic distribution would be again appropriate and lead to some symmetry in the sampling distribution about the projection of the horizon line.

c) Constant Size Resolution Along the Longitudinal Plane

A further theoretically possible distribution exists if the information array for the eye is the terrain surface and contents treated as

> a complex symmetrical, two dimensional pattern viewed from an angle such that its retinal or photographic image is not symmetrical. It will be economical to transmit a description of the pattern as if it were in the frontal plane and symmetrical (eliminating the redundancy of symmetry ...)

(ATTNEAVE, 1954).

To effect such optimal sampling in the longitudinal plane the sampling provision must be the same for unit distance along the terrain regardless of its distance from the eye. The local sampling rate must therefore vary inversely as the square of its angular elevation above the image of the horizon line [the square relation arises from oblique viewing of the surface (BAIRD, 1970)]. Such a distribution would convert the longitudinal into a pseudofrontal projection of the terrain and compensate for perspective distortion.

d) The Quantitative Description of the Real Visual Streak

The above analysis suggests acuity profiles matched to several invariant features of the retinal image. Under optimal conditions the sampling density profile should be matched to the predicted acuity profile by the sampling theorem. If all retinal ganglion cells are of classes to which the above analysis applies then the ganglion cell density profile in some species may have one of the predicted forms; if not, the models will be applicable only to the distribution of the appropriate subclasses. If the system is subject to other influences, such as the lattice noise discussed in Section E III, then the number of independent samples predicted by the model will be less than the number required by the systems' degraded sampling efficiency. A direct comparison of the predicted and actual acuity distributions is currently possible for man alone; comparison of the above models with ganglion cell distributions is the only possibility for other species.

The constant angular-resolution model described above is approximated by the relatively uniform ganglion-cell distributions to be found in a few diurnal and nocturnal retinas, but no species has been encountered with a visual streak whose vertical-sampling profile falls off as the predicted $1/\theta$ or $1/\theta^2$. However, the above analysis may have been in vain; in both monkey and man the behaviorally determined acuity varies as the ganglion-cell density rather than as its square root. *If* such apparent "oversampling" occurs in other species then matching of the ganglion-cell distribution to the information array would require the streak *density*, rather than linear sampling, profile to fall off as $1/\theta$ or $1/\theta^2$ for the two models above. Of these, the former distribution has been observed in the rabbit retina (Fig. 22b).

The vertical-density profile of the visual streak in the majority of examined species does not match the models outlined above, and only slight compensation for the influence of the law of visual angle could be effected by them. On the basis of the assumptions made earlier, the visual streak may be regarded as transforming the spherical isoacuity shells of the space about an eye with a uniform retina into a set of oblate spheroid shells which are more appropriate to objects distributed over an extended terrain (Fig. 22a). However, even for the rabbit, in spite of the form of the density profile, it is not obvious whether the streak may be understood to provide strictly quantitative constant size resolution over a limited range of space or partial compensation over a greater region. The finite peak density of a real visual streak means that it can provide constant-size resolution only to the distance, d_t, which is uniquely determined by the angle subtended by the half value of the density profile. In the rabbit this angle is such that the peak must project at a declination of 2.3°; strict compensation would then occur from the animal to a distance of $28h$; beyond this, resolution would deteriorate. As pointed out previously, this distance is too short for the streak to be effective in dealing with the normal objects of an animal's environment, and it seems more probable that the peak count is directed toward the horizon with only partial offsetting of the influence of the law of visual angle.

It is clear from the proportional relation between θ and h that the terrain from infinity to some distance d will subtend a smaller angle when h is small. If the streak is organised to play a role in offsetting the influence of the law of visual angle on the absolute size of the minimum separabile, then it is a necessary consequence that the half-height, half-width of the streak profile will be narrowest in species with the eyes just above the terrain surface, intermediate in low species such as rabbit, and widest in tall forms such as sheep and horse. The actual presence of such a difference between distributions, with the sheep half-height width at 20° and that of the rabbit at 5.6°, is substantiation of the role suggested for the streak in the model above. The anakatabatic region in the temporal retina of grazing species, which provides increased resolution of the terrain from which food is taken and the feet placed during locomotion, is more elevated in tall than short species.

The above discussion is centered on the role of the streak in the resolution of static features of the environment, but it does not follow that it plays no part in movement detection. Both resolution and the displacement threshold vary in man according to the local ganglion-cell density. MUNK'S (1970) emphasis on the streak as providing high sensitivity of movement for the detection of predator or prey rather than as simply increasing resolution is thus apparently unnecessary, because the former may be consequent upon the latter.

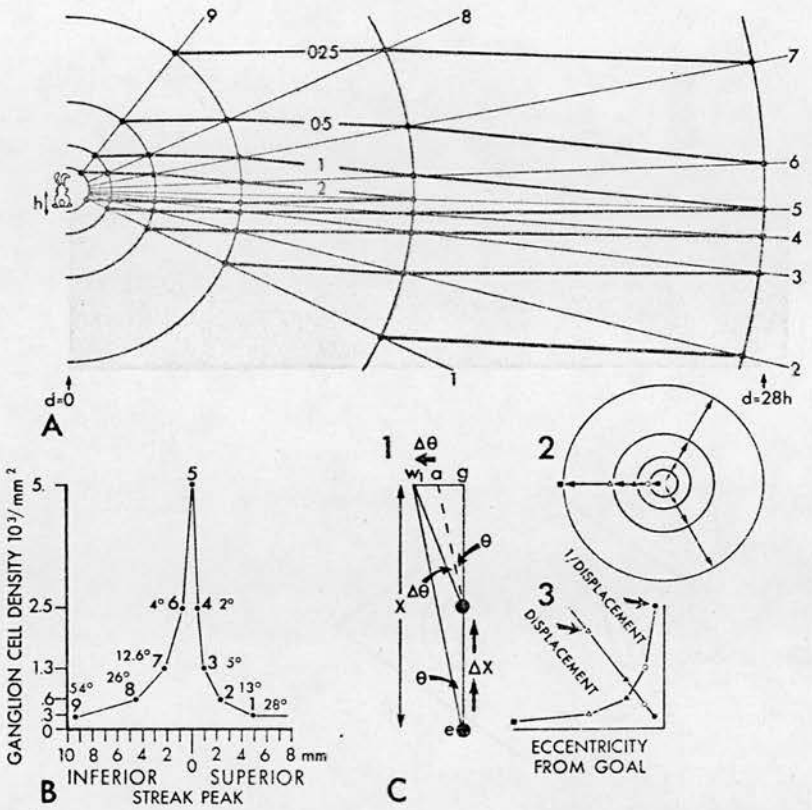

Fig. 22a–c. Vertical cross section of rabbit visual streak ganglion-cell density distribution is shown in (b). Projection into the visual field of points at which ganglion-cell density is successively halved, 5, 6, 7 etc., and 5, 4, 3, etc., is shown in (a) as a series of correspondingly numbered lines which radiate from rabbit eye at height, h, above ground surface. Series of arcs centered on the eye are situated at successively doubled distances. Bold lines thus join angular points in space at which the projected ganglion-cell density is the same. *If ganglion-cell density determines acuity in the rabbit*, as appears to be true for man, then bold lines define profiles along which *absolute size* of minimum separabile is constant. Decline of ganglion-cell density along a rectangular hyperbola in superior retina ensures that if the peak density projects to the ground at a distance $28h$ away from eye, then the inferior borders of absolute-size isoresolution profiles lie parallel to the surface. Thus, local absolute size of the minimum separabile along surface would remain invariant with distance, and the influence of the law of visual angle on resolution is compensated for up to the distance, $d = 28h$. Benefit of this arrangement is very limited at such short distances, and it seems more probable that complete compensation is not employed but the streak rather projects to horizon. Arcs represent constant-size, minimum-separabile profiles for a retina with uniform ganglion-cell density. The more appropriate form of rabbit profiles for a species confined to a terrestial habitat is immediately apparent. [c (1)] Plan view of an eye, e, moving towards a goal, g, in a frontal plane which contains a point w_1. [c (2)]. A representation of image shell in eye, e, which contains the frontal-plane image during such movement. [c (3)] Angular displacement of a series of points in the frontal-plane image shell, c (2), as a function of their initial eccentricity when distance of eye from frontal plane changes by an amount, ΔX. If eye approaches frontal plane containing its goal, g, then for a displacement, ΔX, image of point w_1 will appear to be displaced radially, c (2), from image of goal by an amount, $\Delta\theta$, which is proportional to its initial eccentricity from goal, [c (2)] and [c (3)]. Angular resolution required to detect flow, $\Delta\theta$, of a given image point upon a given displacement, ΔX, of the eye decreases proportionally to eccentricity from image of goal. The equivalent acuity thus falls off along a rectangular hyperbola, $k\ 1/\Delta\theta$, [c (3)], just as the human acuity profile (WERTHEIM, 1894). If the human eye fixates its goal, then a displacement of the eye, ΔX, which produces a liminal image flow, $\Delta\theta$, near to fovea would also produce liminal flow in all parts of the retina served by such an area

That retinal topography is adapted to the information array of the visual image is strongly supported by the singular retinal organization of two species of cyprinodontid fish (MUNK, 1970). These animals possess a lateral streak which projects to the visual horizon and presumably deals with the stream bed. In addition, there is a second, parallel streak which projects its peak density at an elevation of 40° above the horizontal to deal with a 97° diameter circular field above the fishes' head. The retinal region between the two streaks is relatively disorganised and appears almost free of retinal ganglion cells.

The explanation of this arrangement appears to be that these fish are surface feeders for whom events above the water surface form an important part of the information array. Light rays entering the water are refracted at the surface according to SNELL's law, which means that a 180° range of incident rays is compressed by refraction into some 97°. Compression is most marked for the region of field close to the water surface where insects abound and least for that overhead. The ganglion-cell distribution thus appears organised to provide high resolution in the region of greatest image compression and to invert the influence of SNELL's Law on the absolute size of the minimum separabile. The disorganized region of retina between the two visual streaks accepts rays from the stream bed which are subject to total internal reflection at the stream bed which are subject to total internal reflection at the surface, a possible source of confusion to the fish if analyzed in detail.

V. Teleology of the Circumscribed Area Centralis

Certain species, such as squirrels, have long been described as possessed of "universal macularity" because of the relatively uniform organization and high ganglion-cell packing densities of their central and peripheral retina. However, when the small size of these eyes is taken into account, their high ganglion-cell densities are seen to be necessary for even moderate resolution; in all species which attain high *angular* resolution the retina appears to develop a circumscribed area centralis. Such a region is commonly but a few degrees in diameter, and it has been suggested that more extensive distributions are precluded by their concomitant requirement for a greater area of visual cortex for the analysis of their output.

If present in *mammals*, the area centralis is situated centrally in frontal eyes and temporally in lateral eyes; when the eyes are close to the anatomic position of rest, it invariably projects into the binocular field and is so placed as to obtain the image formed by parallel rays from the intersection of the horizon with the median plane. This region of the image is unique in that it contains the goal during forward linear motion, and the presence of a retinal area capable of high resolution could be of obvious benefit.

The circumscribed area centralis, unlike the visual streak, has attracted little discussion concerning the teleologic basis of its form. In man (OPPEL, 1965), goat (HUGHES and WHITTERIDGE, 1973), and cat (HUGHES, 1975b) the ganglion-cell density profile of the area centralis is well approximated by a rectangular hyperbola. Although the isocount lines of these areas are not usually circular, their symmetry about the peak count is very pronounced. It is improbable that these features are without functional significance; the great variety of ganglion-cell distributions so far described argues against their arising simply as a by-product of the morphogenic process.

During forward locomotion, the images of points which make up the bounding surfaces of objects describe well-defined trajectories which are a function of their position relative to the image of the goal. Such *optical flow* (GIBSON, 1966) is radially symmetrical about the image of the goal, and the image flow pattern is thus centered on the area centralis when the goal is fixated. It is suggested that the high degree of radial symmetry in the density profile of the area centralis is an adaptation to this relatively common dynamic information array; some quantitative support for this thesis is available.

Let the goal of a rectilinearly moving animal be contained within a frontal plane at distance x. Two points in the plane which are separated from the goal by distances w_1 and w_2 will subtend angles θ_1 and θ_2 according to the ratio defined by $\theta_1/\theta_2 = w_1/w_2$. If the distance of the eye from the frontal plane changes by an amount Δx (Fig. 22c1), then the image of a given point moves across the retina along an axis with its origin at the image of the goal (Fig. 22c2). The incremental magnitude of this image displacement, $\Delta\theta$, is proportional to the initial separation, θ, of the point from the image of the goal (Fig. 22c3); optical-flow velocity is thus zero at the goal image and increases proportional to eccentricity under these conditions.

Now in the eye of man under photopic conditions not only acuity (WERTHEIM, 1894) but also sensitivity for movement (BOURDON, 1902; AUBERT, 1886) decline along a rectangular hyperbola with

increasing eccentricity from the fovea. When expressed in terms of threshold rather than sensitivity (WEYMOUTH, 1958), this simply means that the angular subtense of both the minimum separabile and limen for movement detection increase proportional to eccentricity. It therefore follows that if a man fixates his goal during rectilinear motion then the radially symmetrical image flow pattern overlays a retinal distribution of movement sensitivity (MC'COLGIN, 1960) which closely matches its form. Thus, for man, *a displacement of the eye perpendicular to the frontal plane, Δx, which produces a liminal image flow near to the fovea would also produce a liminal flow in all parts of the retina served by such an area.*

It is well established for man that optic flow patterns are important cues to the organisation of the visual environment (GIBSON, 1950, 1966). It is obvious, however, that under normal conditions the locomotion-induced flow patterns of the retinal image are much more complex than those analyzed above (GORDON, 1965; KOENDERINK and VAN DOORN, 1975; NAKAYAM and LOOMIS, 1974); objects at varying distances, the longitudinal extension of the terrain, and failure to fixate the goal may eliminate the symmetry of the flow pattern or its matching to the retinal limen distribution. Nevertheless, if the above flow pattern is a stochastically significant feature of the retinal image about the fixation point, then it may be economical to eliminate its inherent redundancy by distributing the available ganglion cells, which are concentrated in the region for the provision of increased resolution, according to the above profile.

The lack of behaviourally determined acuity profiles for species other than man, and the difficulties encountered in attempting their derivation from the ganglion-cell distribution, make it impossible to decide whether the above hypothesis is applicable to other forms whose area centralis ganglion-cell density profile approximates a rectangular hyperbola. That an area may evolve which is not adapted to the radial flow pattern discussed above is indicated by the presence of lateral areas in some birds. Such areas may be primarily concerned with the provision of increased resolution and would not be expected, under the above hypothesis, to show the same distribution of acuity as a frontally projecting area. At present, nothing is known of the behavioral potential of lateral areas in birds, and their quantitative anatomy has only been subjected to preliminary examination (FITE and ROSENFIELD-WESSELS, 1975).

The high ganglion-cell density of the area centralis is thus suggested to have the role of increasing both static and dynamic resolution, but the form of the density profile is hypothesised as matched to the *differential* of the image during goal-fixated forward locomotion. It might be suggested that the density profile of the visual streak is not for the compensation of the effects of the law of visual angle in the eye of the static animal but is rather matched to the flow pattern in lateral-eyed species during forward locomotion. In this instance, however, the lowest density in the streak would be that projecting laterally and the highest to front and rear in a distribution not encountered thus far.

E. Visual Acuity

I. Theoretical Resolving Power

Most visual behavior, especially that encompassed under the term pattern recognition, is beyond the scope of this chapter because its understanding mainly involves parameters of the CNS. The optic and neural factors discussed here rather define the bounds of possible performance in visual behaviour. Traditionally, visual acuity has been a popular topic for interpretation in morphologic terms; many problems remain, however, as will become obvious in due course.

PIRENNE (1962) defines visual acuity as

> the reciprocal of the visual angle, in minutes, subtended by the smallest detail which can be seen under given conditions.

Both he and OGLE (1969) give good general discussions of parameters influencing its magnitude. Many kinds of acuity may be established according to the nature of this detail: alignment acuity (SALOMON, 1947), parallelism acuity (ANDREWS, 1967), curvature acuity (OGILVIE and DAICAR, 1967), vernier acuity (BERRY, 1948), and stereoscopic acuity (BERRY, 1948), among others. Acuity is thus an operationally defined feature of an animal's behaviour which may vary with conditions of measurement, such as the level of illumination, and is determined by optic, retinal, and central factors. Most of the above types of acuity are predominantly determined by central factors (ANDREWS et al., 1973), have unknown mechanisms (WESTHEIMER, 1976, 1977) and thus, although dependant on retinal organisation, reveal little about it and have not been systematically investigated in other species. These *hyperacuities* (WESTHEIMER, 1975) enable discrimination of differential spatial localisation in the order of a few seconds of arc, much finer than the minimum photoreceptor separation, and at first consideration appear to be beyond the capabilities of the optical or neural apparatus. Hyperacuity is unrelated to the super-resolution mentioned below, in which the diffraction limit in the image may be locally exceeded, and is not to be confused with 'aliasing' in which the presence of a periodic stimulus can be detected by a receptor array spaced at some sub-harmonic interval, although it cannot be resolved in the usual sense. Such a phenomenon is only possible when the optical quality of the image is better than that of the sampling matrix and thus might be demonstrable in peripheral retina or when viewing interference fringes which enable optical limitations to be bypassed. Reports of anomalous resolution in insects (BURT and CATTON, 1962) were suggested by BARLOW (1965) to arise as edge effects when stimulus gratings were moved past a frame; since then no technically unchallengable evidence in support of anomalous resolution has been put forward (see HORRIDGE, 1975). Aliasing or anomalous resolution may account for phenomena observed with high frequency interreference gratings of period below that detectable via the optical apparatus of the eye (BYRAM, 1944). In fact, some of the improvement in resolution encountered with such fringes at the fovea may result from inability to see the transition from cut-off frequency resolution to 'presence' detection in the tiny visible region of grating (CAMPBELL and GREEN, 1965). Certain other 'so-called' acuities which establish a *minimum visibile* are neglected here because they reduce to a brightness discrimination task (HECHT and MINTZ, 1939; PIRENNE, 1962) rather than one of identification of the spatial location of stimuli. This discussion is thus limited to relating the *minimum separabile* to morphologic features of the eye and is centered on acuity established from static grating-pattern stimuli for which a few comparative results are available. Results obtained with the Landolt C pattern cannot be compared, because this amounts to a minimum visibile task and gives quite different results to grating acuity in man (SHLAER, 1937; MILLODOT et al., 1975). For a retinal illumination of 3.2×10^3 trolands, a Landolt C gap of 28″ is resolvable compared with a grating-bar width of 35″. In man, at least, it has been shown (GILBERT and FENDER, 1969; WESTHEIMER, 1972a) that visual acuity with a stabilised retinal image is only very slightly lower than for that measured with a freely moving eye. No consideration of dynamic acuity is therefore presented in the following discussion but it has been treated in some detail by DITCHBURN (1973).

It has already been pointed out that the image of even a diffraction-limited optic system has an inherent grain, because any point in object space gives rise in the image plane to a light distribution of finite and irreducible dimensions, the *Airy Disc;* for a human eye with an optimal 2.0 mm pupil (WOODEHOUSE, 1975), $\lambda = 555$ nm and $\mu_0 = 1.336$ the Airy disc is 52″ in radius. Under other conditions of illumination, it has been demonstrated that the natural pupil diameter is optimized to give the best possible behavioural resolution (CAMPBELL and GREGORY, 1960; WOODEHOUSE, 1975).

The optic resolving power of the eye is often defined in terms of the RAYLEIGH (1879) criterion, according to which the images of two point sources cease to be resolvable when their centers are separated by the Airy disc radius, and the summed intensity distribution evinces a 26% trough between its peaks. The assumption of such a degree of limiting contrast is arbitrary, and the true value for any system depends upon the nature of the receptor which is employed to examine the intensity distribution. The SPARROW (1916) criterion, achieved when the Airy discs are separated by 0.78 or less of their radius, is sometimes presented as a limiting condition in which resolution is impossible, because there is no trough in the summed intensity distribution (Fig. 15). For a 2-mm pupil the optic resolving power is thus 52″ according to the Rayleigh criterion and 40″ according to the Sparrow criterion. Two-point discrimination is, however, more complex than implied by such an approach, and its inadequacy as a basis for specifying resolution has been emphasized by TORALDO DI FRANCIA (1955) who writes

> one cannot escape the discouraging conclusion that a very common sentence like: The resolving power of such an instrument has such a value has no meaning. Resolving power is not a well-defined physical quantity.

The summed intensity distribution for two points, no matter how close they are to one another, is always theoretically different from that for one point, and is thus subject only to practical limitations on its discrimination. The consideration of limitations on resolution thus requires a more general approach. The fundamental *invariant* which limits the information capacity of an optic system is its number of degrees of freedom defined in terms of the two-dimensional spatial band width, object area, polarization states, temporal band width, and observation time. An increase in the performance of one of these components may be attained upon the surrender of capacity from another. Super-resolving systems which exceed the classic resolution limit are thus possible if the object field is restricted. A theoretical and experimental discussion of such systems is available (BACHL and LUKOSZ, 1967).

However, when information is *uniformly* distributed throughout the image space, a straightforward and theoretically sound basis for the definition of an optic minimum separabile is possible. According to the Fourier approach discussed above, we know that the image cannot contain a spatial frequency component greater than the MTF cut-off frequency defined by the optic system's PSF width. The minimum separabile thus cannot be smaller than the period of an extended sinusoidal grating of cut-off frequency, because the contrast between the peaks and troughs of the intensity distribution is then zero.

The *attainment* of even this degree of resolution is, however, dependent upon the receptor distribution. HELMHOLTZ (1924) first pointed out that between two

Table 5

	Man		Cat		Rat	
MTF. cut-off frequency	60	cycles/°	20	cycles/°	4.6	cycles/°
RMF	0.291	mm/°	0.222	mm/°	0.06	mm/°
Theoretical necessary sampling density for optic information	179000	mm²	32000	mm²	24000	mm²
Cone density	150000	mm²	25000	mm²	4000	mm²
Theoretical cone cut-off frequency	56	cycles/°	17.5	cycles/°	1.86	cycles/°
Ganglion-cell density	150000	mm²	10000	mm²	6000	mm²
Theoretical ganglion-cell cut-off frequency	56	cycles/°	11	cycles/°	2.3	cycles/°
Behavioral cut-off frequency (acuity)	64	cycles/°	6	cycles/°	1.5	cycles/°

Sources (man, cat, rat, optimal values, respectively): MTF.: CAMPBELL and GREEN (1965); ENROTH-CUGELL and ROBSON (1974); 1-mm pupil: HUGHES (1976); RMF.: LE GRAND (1967); VAKKUR and BISHOP (1963); HUGHES (1977c); Cone density: ÖSTERBERG (1935); STEINBERG et al. (1973); HUGHES (1977c); Ganglion-cell density: 1:1 cone to ganglion cell assumed, see BOYCOTT and DOWLING (1969), MISSOTTEN (1975), HUGHES (1975b), and HUGHES (1977c); Behavioural acuity: SHLAER (1937), BLAKE et al. (1974), and HERMANN (1958).

potentially resolvable image points a further receptor must be interdigitated to detect the reduction of intensity between them. This result is essentially that pronounced in the sampling theorem of CAUCHY and SHANNON (YEN, 1956; CAUCHY, 1841; SHANNON and WEAVER, 1949); a one-dimensional distribution is completely specified by its amplitudes at successive intervals of $1/2f$ if it has no Fourier components of higher spatial frequency than f cycles per degree. The resolution of the 52″ two-point separation of the 2 mm pupil RAYLEIGH criterion thus requires receptor spacing of 26″. The sampling theorem is readily extended to deal with a two-dimensional distribution, such as the retinal image, for which it may be shown (REZA, 1961; BRILLOUIN, 1962) that all of the available information may be recovered from a *square* sampling matrix with receptor spacing of $1/2f$ degrees as above. A more realistic hexagonal array may be shown to be optimal with a somewhat greater spacing of $1.15/2f$ (PETERSON and MIDDLETON, 1962; SNYDER and MILLER, 1977b).

It is thus possible, given the MTF or PSF of an optic system, to estimate its cut-off spatial frequency, f cycles/degree, by means of extended gratings and obtain the minimum retinal sampling density adequate to recover all the spatial information present in the image. Correction is required if the test fields are of limited extent (SIMON and DENIEUL, 1973). A comparison of the theoretical and actual sampling density of the cone or ganglion-cell distributions indicates whether the potential resolution of the optic system could be approached by the neural apparatus—but, of course, does not indicate whether it is. Sufficient information is available to permit this exercise to be carried out for only three species of mammals (Table 5).

Persons of analytic disposition, and I must confess to have one with "too strict an incredulity" in mind, are commonly unsatisfied with attempts to apply the sampling theorem to real systems because they find the conditions of its mathematical derivation immediately unsatisfied. Certain problems may arise simply from incomplete statements of the theorem such as that above, which omits reference to signals at the cut-off frequency, f_c. In an excellent treatment of the subject BRACEWELL (1967) presents a more complete version of the theorem,

A function whose Fourier transform is zero for $|f| > f_c$ is fully specified by values spaced at equal intervals not exceeding $1/2 f_c$ save for any harmonic terms with zeros at the sampling points.

but equal intervals are not obligatory; irregularity in the sampling points is not necessarily, but may be (BRACEWELL, 1965; FRENCH et al., 1977), detrimental to performance and does not preclude theoretical treatment (YEN, 1956). Inability to meet the requirements of ideal bandlimiting is more often seen as a barrier to application of the theory. However, the whole conception of bandwidth limitation as applied to real systems is essentially paradoxical (SLEPIAN, 1976); a bandwidth limited signal must be infinite in duration and a finite duration signal must be infinite in bandwidth, yet we commonly deal with signals as if of both finite duration and limited bandwidth. Clearly the practical application of these concepts requires consideration of the *effective bandwidth* of a signal specified by some upper frequency beyond which its energy is small enough to be ignored with a resultant error acceptable in the system under consideration (CHIRLIAN, 1967). It is noteworthy that the diffraction limited image is one in which there really is an upper cut-off-frequency above which there is zero modulation.

Photoreceptor densities and optical image quality in homeotherm eyes are such that undersampling at this layer is improbable. Available data does suggest, however, that optical quality may be superior to the sampling capability of the retinal ganglion cell array in the central areas of most species, and the periphery of all. If the ganglion cell had direct access to the image plane then the effect of this would be to cause the periodic upper sidebands in the frequency domain (BRACEWELL, 1965) to overlap the distribution centred on zero frequency with consequent inability to recover the spectrum of the original signal and resultant distortion. However, such a result may be quite acceptable in some systems and, in any case, it is apparent that the ganglion cell layer may well be matched to the optimal image of the overlying retina by a neural low pass filter compounded in the prior stages of retinal processing. It remains to be seen whether the cut off frequency of retinal ganglion cells involved in resolution tasks is matched to their local density or to the image quality, when it is superior in resolution.

Other limitations such as the inevitable restriction of the system to a finite array introduce further sources of distortion but these can be small and are discussed by BRACEWELL (1965) and by DITCHBURN (1976) in a lucid and brief account. More important from the point of view of practical application of sampling theory is consideration of retinal noise and photon noise which, at all realistic light intensities, may swamp the tiny modulation of the sampling aperture resulting from signals above cut-off-frequency. A compact discussion of the design requirements for maximising signal to noise ratio in a diffraction limited retina has been provided by SNYDER and MILLER (1977b).

Tentatively accepting the data upon which Table 5 is based, we may conclude that the foveal photoreceptor and ganglion-cell matrix of man are closely matched to the quality of the retinal image (see also BURTON, 1973); the match is also good for the cat photoreceptor matrix, although not for its ganglion-cell distribution, and is poorer still for both rat photoreceptor and ganglion-cell matrices. As suggested earlier, the behavioral cut-off frequency is most closely related to the theoretical ganglion cell cut-off frequency but, of course, this is demonstrated above only for the retinal elements near the fixation axis and not those of the peripheral retina.

II. Optical Limitations on Visual Acuity

The direct formation of sinusoidal interference grating patterns in the human retina (LE GRAND, 1937; CAMPBELL and GREEN, 1965; WESTHEIMER, 1960) is relatively uninfluenced by the refractive state of the eye and may thus be employed to determine the resolution of the neural visual apparatus with the optics "short-circuited." Comparison of a contrast sensitivity function determined this

way with one obtained by direct viewing of a sinusoidal grating enabled CAMPBELL and GREEN (1965) to establish that nearly one-third of the loss in contrast of high-frequency components of the retinal image arose in the human *foveal* region from the limitations of the optic rather than the neural apparatus. A subsequent examination of more eccentric temporal perifoveal images by GREEN (1970) indicated that up to 4° from the fixation point the image quality was poorer for normally viewed than for interference gratings (Fig. 23–4 + 5). At greater eccentricities he concluded that optic quality was of little significance in limiting the performance of the subjects employed.

MILLODOT et al. (1975) report that the correction of refractive errors has no influence on peripheral grating, or Landolt C, acuity. By contrast, LEIBOWITZ et al. (1972) describe considerable improvement in peripheral-movement detection thresholds after vertical and horizontal cylindrical refractive corrections, but such corrections were not necessary in all subjects. Oblique astigmatism was not compensated and could play an important part in limiting performance under natural conditions. It is important to realise, however, that image quality is not simply determined by focus and that diffraction, scatter, etc., may play important roles. An investigation of the peripheral retina at 20° to 70° eccentricity by means of the interference technique (FRISEN and GLANSHOLM, 1975) contrasted with the findings of GREEN (1970) in attributing a reduction of peripheral acuity of up to 40% to optic factors. Of course the absolute quality of the retinal image is not established by this method, and it must have undergone considerable deterioration relative to that on the optic axis in order to have such influence on the much-reduced peripheral neural acuity. This view is substantiated by the preliminary human peripheral LSF measurements of RÖHLER (1962).

For the remaining mammals there is little direct experimental information about optic limitations on resolution. According to BONDS (1974), the sensitivity profile of some cat retinal ganglion-cell receptive fields is so narrow as to be necessarily defined by the PSF; the theoretical treatment of WÄSSLE and CREUTZFELDT (1973) shows that the receptive-field diameter measurements require significant correction for optic blurring if less than 15′ in extent even in the central field. The 135-fold range of pupil area of the cat (WILCOX and BARLOW, 1975) means that the optic limitations on neural resolution will vary significantly with the natural pupil size. The LSF determined by ENROTH-CUGELL and ROBSON (1974) appears narrowest for a 1 mm pupil at 2.8′ half-height width in contrast to BONDS' claim that image quality reduces again for pupils less than 3 mm wide. It is improbable, for the theoretical reasons outlined previously, that the cat should suffer in behavioral resolution because of optic factors when the pupils are 1–3 mm in width. However, BONDS (1974) points out that for larger pupils the best retinal ganglion cell MTF obtained by ENROTH-CUGELL and ROBSON (1965) is of inferior quality to the optic MTF with a 4.5 mm pupil but superior to that with a 13.5 mm pupil. CAMPBELL et al. (1973) report that the evoked potentials at the cortical projection of the area centralis establish a contrast-sensitivity function which drops to 4% at 5 cycles/°, a frequency at which BONDS' optic MTF for the cat is only reduced to 60%, and conclude that the optic quality of the cat retinal image is much better than the resolving power of its visual system. However, the validity of this conclusion is doubtful, because CAMPBELL et al. (1973) employed a 6 mm pupil, yet compare their results with those BONDS obtained with a 3 mm pupil. The difference in pupil size can have substantial implications; the MTF for one of BONDS' cats dropped to 5% (BONDS, 1974) at 5 cycles/° for a 3.0 mm-wide pupil but only attained 2.5 cycles/° with a 4.8 mm pupil. A 6-mm pupil would thus impose a significantly greater limitation on the overall cat contrast-sensitivity function than a 3-mm pupil. The behavioral contrast-sensitivity function obtained for the cat by BLAKE et al. (1974) would be even more subject to influence by optics than that of CAMPBELL et al. (1973).

According to BONDS (1974), the peripheral optic quality of the cat eye is poorer than the central: the LSF increases twofold in width over 15°–30° eccentricity. However, he calculates that the 0.6° LSF

10% width at 30° eccentricity would lead to only a 3% increase in the mean local receptive field diameter of 2.5° (FISCHER and MAY, 1970), and thus peripheral optic factors have little influence on resolving power.

HUGHES and WÄSSLE (1977) have estimated the rat MTF to have a cut-off frequency of some 13′ with a 0.3-mm pupil and between 25′ and 36′ for a 2.5–3.0-mm pupil. The behavioral acuity of 40′ (HERMANN, 1958) clearly indicates that resolution in this species is unlikely to be substantially limited by the quality of its optics at photopic levels of illumination.

III. Neural Limitations on Visual Acuity

The decline of visual acuity with increasing eccentricity from the human fixation axis has been subject to numerous attempts at explanation in morphologic terms since its first detailed description by AUBERT and FÖRSTER (1857). However, current work makes it impossible to agree with the recent statement of LE GRAND (1967) that for man

> it is obvious that the dioptrics of the eye, which are of fairly good quality up to 30° eccentricity, have no effect whatsoever on peripheral acuity,

and the neural component of the acuity gradient requires separate specification. Neither peripheral acuity nor optics has been investigated in other mammalian species, and the topic must be considered almost solely in terms of the organization of the human eye.

The various methods of measuring visual acuity reveal a qualitatively similar gradient across the retina (Fig. 41, LE GRAND, 1967), but under the same conditions the use of the Landolt C consistently indicates higher peripheral values (BERKLEY et al., 1975) than grating acuity. The latter is, however, a more satisfactory measure and amenable to both optic and anatomic interpretation. In spite of this, few measurements of human grating acuity are available, and of these the majority deal only with the temporal horizontal meridian. The descriptions provided by DOR (1873), WERTHEIM (1894), FICK (1898), and BERKLEY et al. (1975) agree quite closely with each other, but the results of WERTHEIM (1894) alone provide complete isoacuity contours for the whole field of vision. These still stand as exemplary work but suffer the disadvantage that they are expressed in relative terms, and the conditions of illumination at which they were obtained is not known. The human isoacuity contours are elliptical, with the minor vertical axis in the ratio of 0.7 to the horizontal axis. Lower field acuity is somewhat greater than upper (WERTHEIM, 1894; LOW, 1943; MILLODOT and LAMONT, 1974). The decline in human acuity along the horizontal meridian in Wertheim's results was shown by WEYMOUTH (1958) to be well fitted by a rectangular hyperbola out to an eccentricity of some 50°. It is thus of interest to see if this form can be explained on an anatomic basis.

Certain difficulties first require outlining. The acuity curve of WERTHEIM (1894) for the temporal retina is shown in Fig. 23—3, in terms of its inverse—the minimal angle of resolution; the bar width or half period in minutes of a just resolvable grating—, where it is seen to be similar in form to the Landolt C acuity curve determined by MANDLEBAUM and SLOANE (1947) at their highest light

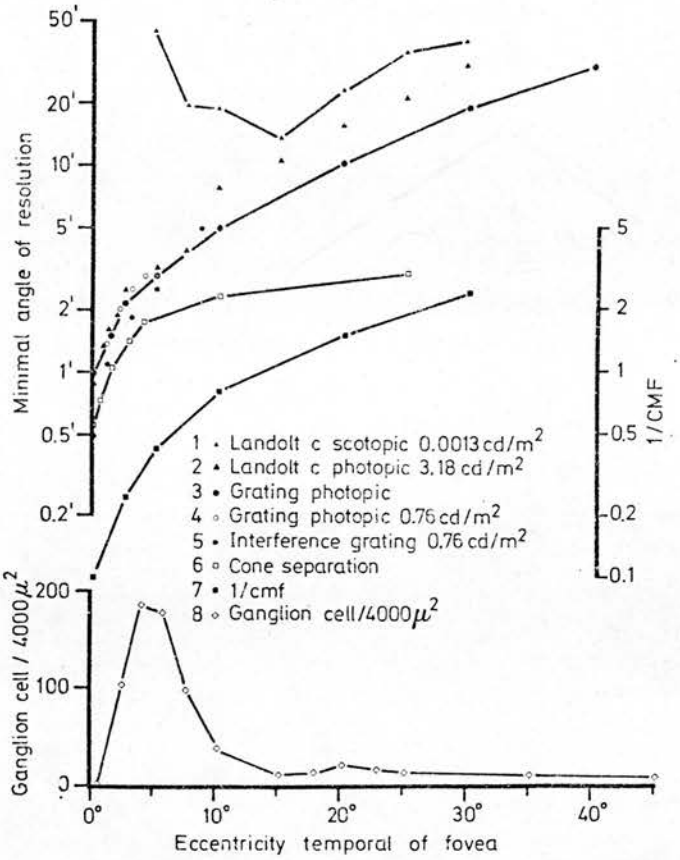

Fig. 23. Minimal angle of resolution—the bar width of a just-resolvable grating—as a function of retinal eccentricity, illumination, and stimulus form. Greater resolution obtained by the use of interference fringes as grating stimuli (GREEN, 1973) indicated that optic quality limits performance of foveal neural apparatus during normal viewing of a grating. Other sources: photopic grating normalized to 1′ acuity, WERTHEIM (1894); photopic and scotopic Landolt C, MANDELBAUM and SLOANE (1947). Cone separation (ÖSTERBERG, 1935) is plotted over the the same range of eccentricity and may be seen to account for neural resolution within some 2° of visual axis. At greater eccentricities, potential resolution of cone matrix is not achieved because of convergence in receptor to ganglion-cell connections. Displacement of foveal ganglion cells to the perifoveal region in man (OPPEL, 1965) makes it difficult to demonstrate a direct relationship between ganglion-cell separation and resolution. However, in other primate species, the cortical magnification factor has been shown to vary as the ganglion-cell *density* COWEY and ROLLS, 1968). The inference that this is also true in man is reasonable; the above demonstration (COWEY and ROLLS, 1974) that the reciprocal of the CMF varies as the minimal angle of resolution thus indirectly supports the thesis that human acuity varies as ganglion-cell *density*

intensity (Fig. 23—2). It is to be emphasised that both of these curves change as the light intensity is reduced (MANDLEBAUM and SLOANE, 1947) into the scotopic range where, as in Fig. 23—1, the resolution becomes fairly constant across the entire hemifield. A morphologic explantation attempts only to deal with extreme photopic conditions and cannot encompass the functional reorganisation of the retina. The illumination sensitivity of the acuity curves also introduces the possibility of obtaining low peripheral acuity readings because of the reduction in

illumination intensity arising with oblique-ray incidence and the reduced apparent pupil size (WEALE, 1956).

It is characteristic of attempts to account for acuity in anatomic terms that only *retinal* structure is considered, but it is obviously possible that subsequent stages in the visual pathway set their own limitations, and this has been demonstrated to occur. Thus, acuity for vertical or horizontal gratings is the same at a given region of the visual field over a range of some 25° from the fixation axis (BERKLEY et al., 1975), but acuity for oblique gratings is markedly reduced (HIGGINS and STULTZ, 1950; APPELLE, 1972) up to an eccentricity of some 8°–18° (BERKLEY et al., 1975). This "oblique effect" has been denied in infants (TELLER et al., 1974) but recently was claimed at 6 weeks and more convincingly demonstrated at over 13 weeks of age (LEEHEY et al., 1975), so that it may not be environmentally determined. The phenomenon is regarded as neural rather than optic in origin, because it remains when interference fringes are employed as stimuli (CAMPBELL et al., 1966; MITCHELL et al., 1973). Cortical-evoked potentials are found to be greater for vertical and horizontal than for oblique grating stimuli in man (MAFFEI and CAMPBELL, 1970; FREEMAN and THIBOS, 1973), but such a difference was not found in the electroretinogram. Explanation of this aspect of grating acuity is thus sought at the cortical rather than retinal level in terms of the proportions of single units sensitive of specific stimulus orientations (BERKLEY et al., 1975).

Central photopic acuity was first explained in terms of foveal-cone separation by HELMHOLTZ (1924), but extension of the quantitative comparison to the peripheral retina awaited ÖSTERBERG's (1935) account of the human retinal-cone distribution. Several authors [POLYAK, 1941; LUDVIGH, 1941; DOESSCHATE, 1946; (Fig. 43), LE GRAND, 1967] then found satisfactory agreement to extend for only a degree or two of eccentricity, acuity subsequently falling off more rapidly than cone separation (Fig. 23—6). Even when the possibility of optic impairment of resolution is eliminated by the use of interference fringes as stimuli, it is found (GREEN, 1970) that cone separation and the sampling theorem account for the attained neural resolution over no more than 2° from the fixation point.

The accepted conclusion that acuity at greater eccentricities is primarily determined by the local ganglion-cell provision (DOESSCHATE, 1946; WEYMOUTH, 1958) is exceedingly difficult to establish quantitatively in man. WEYMOUTH (1957) employed odd results of POLYAK (1941) to obtain a crude quantitative human ganglion-cell distribution which he related to the acuity gradient. The ganglion-cell distribution map of VAN BUREN (1963) is of little use in quantitative discussion, because it does not provide densities but only the local number of cell layers. A relationship between ganglion cell provision and acuity is, however, apparent in these maps, because their contours are of similar elliptical form to the isoacuity lines of WERTHEIM (1894). No ganglion-cell density map based on a human retinal flat mount is available, but VILTER (1949, 1954) and OPPEL (1965, 1967) provide uncorrected ganglion-cell distributions for a horizontal thin section of human retina (Fig. 23—8). It is apparent that the contamination of ganglion cells connected to perifoveal receptors with those displaced from the fovea makes the comparison between ganglion cell distribution and acuity difficult. Correction for the ganglion-cell connectivity pattern may become feasible (MISSOTTEN, 1974). At

present, it is possible to relate acuity to the ganglion-cell distribution via the cortical magnification factor.

In many species of animal, it has been found that the distance in millimeters devoted to the representation of 1° of the visual field at its projection on some central station of the visual pathway, the magnification factor (MF), is proportional to the ganglion-cell density of the corresponding retinal region: frog tectum (JACOBSEN, 1962), cat LGN, rabbit colliculus (SENEVIRATNE, 1963), cat and baboon colliculus (VEJBAESYA, 1968), cat LGN (SANDERSON, 1971), rabbit colliculus, cortex, and LGN (HUGHES, 1971), and monkey cortex (ROLLS and COWEY, 1970), owl monkey (WEBB and KAAS, 1976). This relationship cannot be regarded as inevitable, because it does not apply to the projection of the visual field parallels onto the rabbit visual cortex. However, ROLLS and COWEY (1970) describe both squirrel monkey and macaque cortical magnification factors (CMF) as proportional to the topographically corresponding ganglion-cell density from 50° to 7° eccentricity and extrapolate from the cone separation to conclude that this relationship applies throughout the perioveal and foveal regions. At present, however, the gradient of monkey visual acuity has not been determined. but DANIEL and WHITTERIDGE (1961) did show that *human* visual acuity varies as the *monkey* CMF and thus (ROLLS and COWEY, 1970) as the *monkey* retinal ganglion-cell density.

More recently, COWEY and ROLLS (1974) have employed the results of BRINDLEY and LEWIN (1968), who plotted the projection into the visual field of phosphenes induced during cortical stimulation at known locations, to determine CMF's for man and to demonstrate their proportionality (Fig. 23—7) to acuity measured at the same eccentricity by WERTHEIM (1894). No satisfactory human ganglion-cell distribution map is available, but the uncorrected results of VILTER (1954) and, to a lesser degree, of OPPEL (1965, 1967) suggest that from 50° to 10° eccentricity the cortical magnification factor varies roughly as ganglion-cell density. The form of the ganglion-cell density/CMF plot is so similar to those for *saimiri* and *macaque* (ROLLS and COWEY, 1970) as to stand as presumptive evidence that proportionality between the two factors may be extrapolable into the foveal region in similar fashion as for the two monkeys (ROLLS and COWEY, 1970).

FRISEN and FRISEN (1976) have recently claimed that the angular frequency of human retinal ganglion cells, corrected for peripheral reduction in RMF, is simply proportional to the corresponding local acuity established by an interference fringe technique (FRISEN and GLANSHOLM, 1975). A similar claim has been made by DRASDO (1977) who reports proportionality between acuity as established by WERTHEIM (1894) and the corresponding ganglion cell frequency, obtained as the mean of data from several orientations in the publications of three authors (VILTER, 1954; OPPEL, 1967; VAN BUREN, 1963) and also corrected for change in RMF with eccentricity. FRISEN and FRISEN suggest that their result should be no surprise; indeed, it is what might be expected a priori from sampling theory considerations! However, it would necessarily follow from their findings, and those of DRASDO (1977), that CMF, because it is proportional to acuity, must also be proportional to the ganglion cell frequency, i.e. the square root of the ganglion cell density. DRASDO (1977) clearly misinterprets ROLLS and COWEY'S results (1970) as indicating this to be true for the monkey and thus in accordance with his conclusions for man; in fact, ROLLS and COWEY report the macaque CMF to be proportional to ganglion cell density and not its square root. If FRISEN and FRISEN (1976) and DRASDO (1977) are correct, it would mean that man is unique amongst the investigated mammals, assuming the validity of earlier data, in failing to have his CMF proportional to ganglion cell density and, perhaps more important, quite different in organisation to the macaque. However, the ganglion cell distribution data employed by FRISEN and FRISEN, and DRASDO, are not of such quality to support confidence in their

conclusions, especially in view of the conflicting indications from other sources. All the data was obtained from thin sections which give unreliable counts (see STONE, 1965); their shrinkages are unknown and probably different; the counts have not been subjected to an ABERCROMBIE correction (ABERCROMBIE, 1946), whose magnitude changes as a function of ganglion cell size with eccentricity; the ganglion cell criteria are unspecified and probably vary between the sources (the values of VAN BUREN differ by at least one order of magnitude from those of VILTER with which DRASDO pools them) and so on. A definitive count is required.

It thus remains almost certain, as suggested above, that the peripheral visual acuity of man and monkey is proportional to the corresponding ganglion cell density and not, as might be expected from elementary application of the sampling theorem, to its square root. Resolution would thus decrease more rapidly with increasing eccentricity than ganglion cell proximity and clearly indicates that *total* ganglion cell density cannot be a limiting factor for human peripheral acuity. It is curious therefore, that the absolute foveal acuity of man is well accounted for in terms of the square root of the sampling density at the receptor and ganglion cell levels (Table 5). The apparent surplus of ganglion cells over the theoretical requirements thus seems to increase with eccentricity from the fovea and suggests the possibility of a progressive change in retinal organisation which follows a simple law.

To avoid the problem of the displaced ganglion cells of the fovea, consider the ganglion cell densities, D, to be expressed in terms of their receptive field densities per square degree instead of perikaryon density on the retina. The theoretical and actual spatial frequency of the image above which the ganglion cell matrix is incapable of resolution, fp, for the peak density of the fovea is then given as $f_p = \sqrt{D_p}/2$ in cy/°. If the cut-off frequency elsewhere on the retina is accepted as falling off proportional to the local ganglion cell density then at the point i it is given as $f_i = (\mathrm{Di}/\mathrm{Dp}).(\sqrt{\mathrm{Dp}})/2$ in cy/° whence it may readily be derived that the ratio of the actual ganglion cell density at the point i to the effective density, De (i.e. that required by an optimal system to obtain the same cut-off frequency, fi), is given by $\mathrm{Di}/\mathrm{De} = \mathrm{Dp}/\mathrm{Di}$. It is possible that various factors interact to give an approximation to this relationship but, if not, we seek a single influence to explain why the local surplus of ganglion cells increases as the ratio of the peak to local density and thus inversely as acuity. Given the previous approximation of the human acuity curve to a rectangular hyperbola it may also be concluded that the surplus ratio increases proportional to eccentricity.

Behavioural acuity on the fixation axis and the corresponding central ganglion cell density are available for five species of mammal thus enabling an examination of the general applicability of the sampling theorem at the visual pole (Fig. 24). Agreement between theoretical and behavioural acuities is fair but the behavioural values for cat and rabbit a significantly lower than the ganglion cell density would suggest. A degree of uncertainty must, however, by inherent in such comparisons. The acuity data of the cat was obtained from the results of BLAKE et al. (1974) which suggest a cut-off frequency of some 6 cy/°; new techniques, BISTI and MAFFEI (1974), MITCHELL et al. (1977), have brought reports of a 9 cy/° cut-off frequency and even higher values have been mooted, JACOBSEN et al. (1976), although accompanied by some curious anomalies. In tests of stripes versus uniform fields, or even of horizontal versus vertical stripes, the animal may be able to detect the presence of the stimulus by means of an 'aliasing' phenomenon because its eye is not diffraction limited. Acuities in the order of 9 cy/° in the cat are close to the predictions based on the total ganglion cell density of the central area being representative for cells involved in resolution tasks. The applicability of the sampling theorem to the *total* ganglion cell density in the cat central

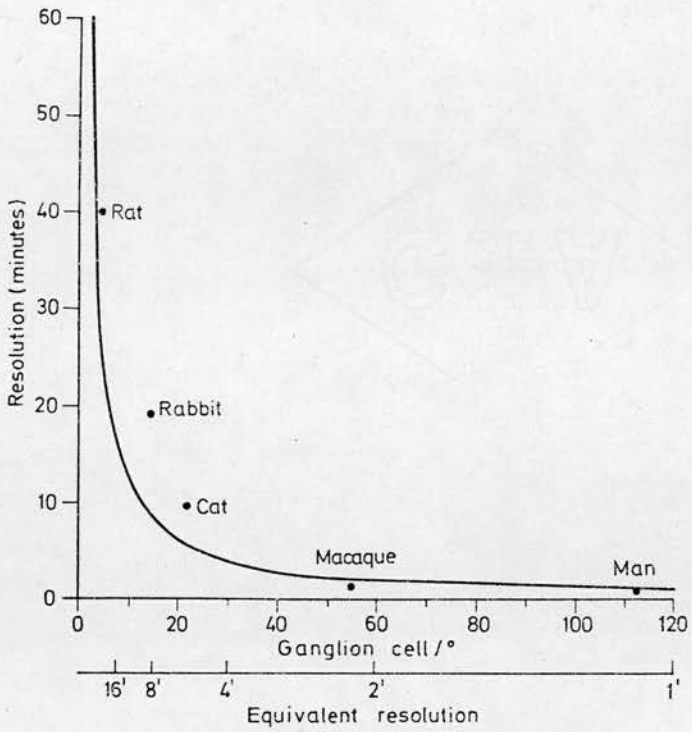

Fig. 24. The points indicate the behaviourally determined grating resolution in min/cycle, plotted against the square root of the ganglion cell density, ganglion cells/°, for the region of retina bearing the highest ganglion cell density on the visual axis. A second scale, equivalent resolution, indicates the width in minutes of the theoretical minimum resolvable grating period determined as [60/(ganglion cells/°)]/2 in accordance with SHANNON's sampling theorem. The continuous line indicates the relationship theoretically applicable if the potential resolution of the ganglion cell density were achieved behaviourally. The deviation from the line is significant for rabbit and cat. Sources: rabbit; VAN HOF (1967), HUGHES (1970); macaque (ROLLS and COWEY (1970); remainder, see Table 5

area thus remains in doubt; the situation in the less well investigated rabbit remains more obscure.

We are thus left with the puzzle as to why there is an apparent *systematic* failure of the sampling theorem away from the human fovea, some doubt as to its applicability in the central area of cat and complete uncertainty as to its relevance in the central areas of other non-primate mammalian species. The peripheral retina of species other than man cannot be discussed in this context as peripheral acuity measurements are not available. The interference fringe method of retinal stimulation indicates that the majority of the peripheral reduction in acuity in man is attributable to neural factors and that a simple explanation of the peripheral deviations from the sampling theorem is not probable in terms of either refractive error or the greater obliquity of the pupil leading to increased PSF width. The oblique angle of illumination of the pupil by peripheral rays reduces the peripheral retinal illumination and might thus lower the measured acuity relative to that obtainable with the same area on axis but this effect cannot

explain the marked deviations from the expected relationship within the central 30° of the retina. Possible sources of this discrepancy are worth discussing in detail because of their more general significance.

1. Nonhomogeneity in the Retinal Ganglion Cell Receptive Field Population

It has long been known that the retinal ganglion cell population of the cat is made up of cells with both *on*- and *off*-center concentric receptive fields (KUFFLER, 1953). Although these two classes have been regarded as involved in resolution tasks, it is not known whether they play independent roles. The description of the rabbit retina contrasted markedly with that of the cat in that at least 40% of the encountered cells possessed nonconcentric receptive fields which could be grouped into about six classes (BARLOW et al., 1964; LEVICK, 1967). The early hints that the cat also possesses nonconcentric receptive fields which could play no part in acuity tasks (RODIECK and STONE, 1965; STONE and FABIAN, 1966) have subsequently been validated. Cat retinal units are now grouped into three major categories which are based upon a variety of classificatory techniques and termed X, Y, and W (STONE and FUKUDA, 1974), or brisk-sustained, brisk-transient, and sluggish (CLELAND et al., 1971; CLELAND and LEVICK, 1974a); within the last group some six subclasses have been described (STONE and FUKUDA, 1974; CLELAND and LEVICK, 1974b) which contain receptive fields similar to all except the orientation selective retinal units of the rabbit. Nonconcentric units have recently been reported in the macaque retina (DE MONASTERIO and GOURAS, 1975), in addition to some 20 varieties of colour and broad-band receptive fields; the extent to which these units are pooled for resolution tasks remains to be determined. Among other mammalian species, the presence of nonconcentric units has been reported in the ground squirrel (MICHAEL, 1968), sheep (HUGHES and WHITTERIDGE, 1973), and rat (HUGHES, 1976).

Of all these receptive field classes, only the category corresponding to the brisk-sustained cells, X cells, of the cat is generally regarded as capable of subserving resolution (CLELAND et al., 1971). The discrepancy between the acuity achieved by a given area of nonfoveal human retina, or of non-primate mammalian central area, and that calculated from its corresponding ganglion-cell density might thus arise simply because such cells form only a fraction of the local ganglion-cell population.

The identification of the proportion of the local ganglion-cell population suited to resolution tasks is a formidable problem. The physiologic rate of encounter of receptive field types does not appear to correspond with the absolute proportion of the population which makes up a given class. This is known for certain in one instance. Morphologic criteria have enabled the retinal ganglion cells of the cat retina to be grouped into three classes termed α, β, and γ, in order of decreasing perikaryal size and axon diameter (BOYCOTT and WÄSSLE, 1974). Various techniques have enabled the identification of these with the three major receptive field classes (STONE and FUKUDA, 1974; CLELAND and LEVICK, 1974a,b). In a detailed study, some 60% of the peripheral receptive fields examined by CLELAND and LEVICK (1974b) are brisk-transient, whereas histologic evidence indicates that only 3% (WÄSSLE et al., 1975) of the total ganglion-cell population is made up of the corresponding (CLELAND et al., 1975) α cell bodies. Attempts to relate the two sets of proportions by corrections based on theoretical considerations (FUKUDA and STONE, 1974) have not proved satisfactory, and the degree to which electrode impedance is involved in selective sampling is disputed (STONE, 1973; LEVICK and CLELAND, 1974).

The three major cat retinal ganglion-cell classes may be distinguished in peripheral retina by means of perikaryal features alone, but in regions of higher ganglion-cell density the ganglion-cell diameter spectrum loses its distinct modes. In these regions the use of an arbitrary transition size to divide the spectrum (FUKUDA and STONE, 1974) of all areas of retina is not justified. However, by this means FUKUDA and STONE (1974) suggest that the proportions of the various classes, especially the α cells, undergo significant change across the temporal retina. By contrast, in a wider ranging study, WÄSSLE et al. (1975) conclude the α cell proportion to remain relatively constant over the entire retina and publish a map of α-cell distribution (Fig. 25) which is not greatly different in form from that of the total ganglion-cell distribution (Fig. 20). ROWE and STONE (1976) have attempted to estimate the proportions of α, β and γ cells in the periphery and visual streak of the cat retina by dividing the soma diameter spectrum of both regions into large, medium and small modes by means of the criterion

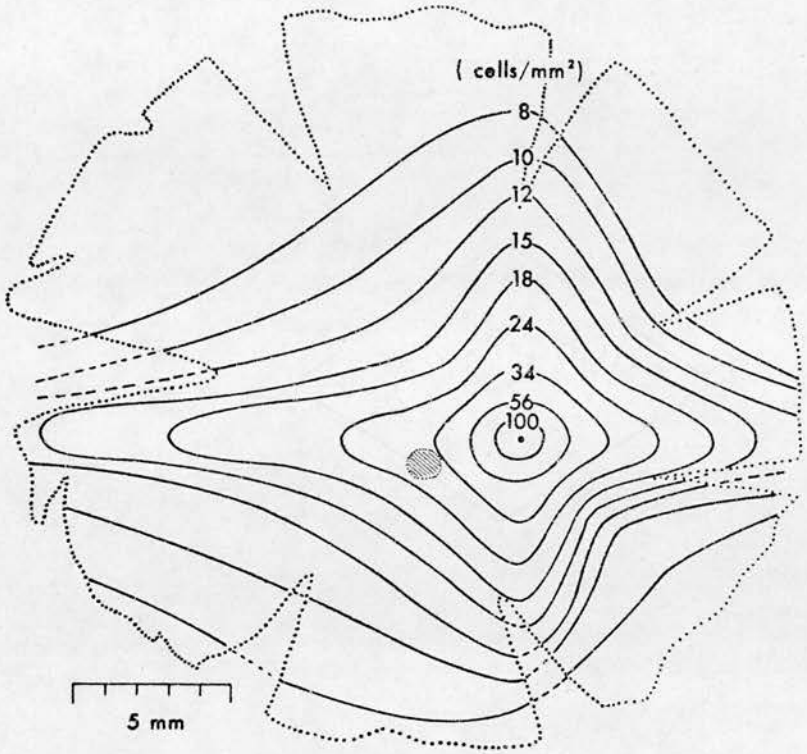

Fig. 25. α-type ganglion-cell density map of a Nissl-stained cat retina showing cruciform distribution which contains area centralis and visual streak. Compare with total ganglion-cell density distribution map of Fig. 20 (Courtesy of WÄSSLE et al. and J. comp. Neurol., 1975)

diameters of 14 μ and 22 μ. They report an increase in the percentage of small cells when passing from the periphery to streak retina in accordance with expectations based upon a similar increase in their electrophysiological encounter rates for units of the corresponding W class. The possibility that the increase in the percentage of small cells indicates, not an increase in the λ cell proportion but rather, a decrease in the β cell mean diameter on the high density streak is dismissed by the unsatisfactory argument that such an increase in the β cell proportion is not to be observed in a region of similar density but adjacent to the area centralis. HUGHES (1978) regards as unjustified the use of peripheral soma criterion diameters in the streak retina and contests the conclusion of ROWE and STONE (1976) that the γ cell proportion increases in the visual streak. The natural criterion for division of the soma diameter spectrum into modes is the dip to be seen between the γ and β modes in all regions, except those of highest density in the streak and area centralis. This method is admittedly subject to error because of the overlap in most regions between the γ and β modes but it is a more satisfactory approximation to the required information than that of ROWE and STONE (1976). Examination of diameter spectra for a sequence of retinal regions which approach either area or streak reveals that the β mode narrows and that its mean moves towards the more constant γ mode mean in agreement with the results of WÄSSLE and BOYCOTT (1975) and quite in keeping with a relatively constant proportion of the classes in spite of a substantial increase in the small cell population. Now ROWE and STONE (1976) report the small cell proportion, which they equate with W units or γ cells, to fall off from nearly 70% on the streak to some 40% below it. By contrast HUGHES (1977e) reports the peripheral γ cell mode to represent up to 65% of the population, a trend suggested by the optic nerve fibre diameter spectra (HUGHES and WÄSSLE, 1976), and finds the proportion to fall in passing to the streak. It is apparent that the peripheral cell densities of ROWE and STONE (1976) are substantially lower than those of WÄSSLE et al. (1975) or HUGHES (1976b) and it appears possible that they do not identify a proportion of the peripheral γ cell

class as ganglion cells. In the central area HUGHES (1977c) reports the γ cell proportion to fall off relative to the streak and WÄSSLE (personal communication), employing techniques for direct identification of cell class, finds that the β proportion amounts to some 70% of the total. Such a value would be necessary from sampling theory if cat acuity is confirmed to be greater than 9.0 cy/° (MITCHELL et al., 1977). The range of density variation of β or, in the inverse sense, of γ cells is thus at least 2:1 across the retina. That encounter rates for given receptive-field classes do differ, in the rabbit between central and peripheral retina (OYSTER et al., 1971) and in the cat between central and peripheral retina (CLELAND and LEVICK, 1974a), and central and streak retina (STONE et al., 1975) is by no means conclusive because of the sampling problem when recording.

It is to be emphasized, however, that the deviation of the behavioral acuity profile by other than a constant factor from that computed on the basis of the total ganglion-cell distribution would not be accounted for by a nonhomogeneous human retinal ganglion-cell population if its composition were uniform throughout the retina. Only a progressive decrease, with increasing eccentricity, in the proportion of the cell class subserving resolution would suffice to explain the observed phenomena without the introduction of other factors.

2. Differential Projection of the Retinal Ganglion Cells

Even if the ganglion-cell population were homogeneous, the theoretical potential resolution could not be attained if the ganglion-cell axons project to different destinations, so that only a fraction of the total population is involved in a resolution task at a given central region. In the cat it appears that the cells most likely to subserve resolution, the brisk-sustained population, project predominantly to the LGN with only minor contributions to other visual centers (CLELAND and LEVICK, 1974; FUKUDA and STONE, 1974). Studies on the retrograde transport of horseradish peroxidase from the cat LGN and superior colliculus to the retina substantiate this differential projection (KELLY and GILBERT, 1975). Similar work on the macaque indicates that the great majority of ganglion cells project to the LGN (BUNT et al., 1975). In these two species and man, at least, the retinogeniculate pathway appears to be the major projection involved in resolution (BRINDLEY, 1970), and the output of the majority of suitable ganglion cells is thus available to the cortex, so that their effective density is not reduced by differential projection.

3. Variation in Receptive Field Size

Not only does sampling theory specify a minimum rate of sampling (2f/°) which is necessary to achieve a given spatial frequency resolution (f cycles/°), but it also indicates an optimum sampling aperture width; apertures smaller than this unnecessarily reduce sensitivity without improving resolution at a given sampling density. Several studies of receptive-field-centre diameter have described a range of sizes within a given region of cat retina (FISHER, 1973) which implies that the system operates non-optimally. However, recent work (CLELAND and LEVICK, 1974) suggests that the range of centre size *for a given class* is more restricted and amounts to only $\pm 10\%$ for the brisk sustained units at the area centralis; such a range would influence the cut-off-frequency, or sensitivity, very little. In the peripheral retina, however, the diameter range increases so that for brisk sustained units it is $\pm 50\%$ at 15° eccentricity. Such a range could limit resolution to an extent dependent upon the relation between its mean and the local optimum diameter: if similarly organized in man it might contribute to the increase with eccentricity in the discrepancy between theoretical and attained resolution but is unlikely to be a major factor.

4. Change in Peripheral Magnification Factor

In most mammalian eyes the PND, and consequently the corresponding local RMF, decreases with eccentricity for chief rays. This phenomenon must be taken into account when estimating the potential maximum resolution to be obtained from a given local ganglion cell density. Measurements of the reduction in RMF have been provided only for the cat eye (HUGHES, 1976a) although theoretical estimates have been made for man which are based upon unverified homogeneous lens schematic

eyes (DRASDO and FOWLER, 1974; FRISEN and FRISEN, 1976; LOTMAR, 1971). The peripheral reduction of RMF is unlikely to be a major factor underlying the discrepancy between the theoretical and measured sampling densities in the human eye because the divergence between the two is well developed within the central 30° of retina where the RMF is relatively constant.

5. Reduction of Sampling Efficiency by a Non-uniform Retinal Mosaic

Irregularity in the sampling matrix need not result in a reduced cut-off frequency relative to an optimal, regular matrix if an appropriate reconstitution function is employed (YEN, 1956). A substantial reduction in the cut-off-frequency will, however, occur if the signals from an irregular lattice are treated as though from a regular lattice; a situation which seems more probable for the eye. A matrix noise such that the standard deviation of sampling position is equal to the mean sampling interval would require a fourfold increase in sampling density if the cut-off frequency of an undisturbed matrix is to be achieved (FRENCH, SNYDER and STAVENGA, 1977). In man, the sampling matrix at the foveal centre is determined by the optimal cone packing lattice; away from this region the constraints on ganglion cell packing are reduced and increased noise in the sampling point distribution might be expected. Under the conditions outlined above this would result in an increasing divergence with eccentricity between the theoretical and attained resolution for a region of given ganglion cell density, just as is found. The matrix of ganglion cell distribution in mammals is certainly not regular for any identifiable class and the degrading influence of such an irregular matrix on the performance of the system at a given ganglion cell density must at least play a part in limiting acuity. Increasing irregularity in the sampling matrix with eccentricity is a strong contender for the explanation of the progressively greater divergence of theoretical and actual sampling density with eccentricity.

A curious relationship arises from the above discussion. Consider two regions of the human visual field with acuities a_1 and a_2, total ganglion cell densities D_1 and D_2, effective densities D_{1e} and D_{2e} and cortical magnification factors in the corresponding regions of area 17 of CMF_1 and CMF_2; then we may write,

$$a_1/a_2 = D_1/D_2 = \sqrt{D_{1e}}/\sqrt{D_{2e}} = CMF_1/CMF_2 \quad \text{and thus}$$
$$(CMF_1)^2/(CMF_2)^2 = D_{1e}/D_{2e}.$$

The cortex being of relatively constant thickness and cell density, it follows from the ratio of cortical area for regions 1 and 2 that the ratio of the number of cortical cells in regions dealing with equal elements of the visual field is in the same ratio as the minimum sampling densities theoretically required to attain the acuities achieved by the areas! The implication is thus that there is a constant provision of some k cortical cells for each independent sampling element at the retinal level. At the human fovea, where the sampling theorem appears to apply directly, it is possible to estimate the value of k as 600 from published cone and cortical cell densities. It seems improbable that several interacting factors, each varying with eccentricity, should result in the properties outlined above; one predominant process would be more likely to lead to such simple arithmetical relationships. A straightforward progressive decrease in the number of sampling points, resulting from a systematic decrease with eccentricity in the proportion of cells involved in resolution tasks, or a loss of independence in the sampling points, as a result of increasing lattice irregularity, would appear to be the major contenders as explanations for the results. Morphological identification of the cells involved in resolution tasks would readily distinguish between the two hypotheses.

IV. Neural Compensation for Optical Impairment of Image Quality

It is a suggestion of long standing that, rather than adding to the optic degradation of image quality, the neural apparatus of the visual system actually compensates for the effects of optic blurring. Originally considered by MACH (1865) as an explanation of subjective border enhancement, this hypothesis has more recently been presented with detailed theoretical substantiation (RATLIFF, 1965). CAMPBELL and GUBISCH (1966), however, find little direct evidence for its general validity *at threshold*. The neural apparatus actually *overcompensates* for optical limitations at low spatial frequencies but in the range above 10 cycles/°, which is important for the definition of spots and edges; the system performance is substantially impaired by the central processing. In agreement with MACH (1865) and BARLOW (1961), CAMPBELL and GUBISCH (1966) conclude that border enhancement is simply a by-product of the mechanism which makes visual sensation independent of average illumination.

The possibility of neural "deblurring" has recently been reintroduced for suprathreshold conditions (HAY and CHESTERS, 1972; GEORGESON and SULLIVAN, 1975). Although a theoretically plausible phenomenon, the evidence in its favor requires cautious appraisal in view of the recent improved estimates of human retinal image quality.

V. The Contrast Sensitivity Function of the Entire Visual System

The form of the MTF for the dioptric apparatus of the eye shows that it transmits spatial frequencies ranging from just below cut-off to zero with equal facility; comparison of such optic systems may thus be readily made by means of their cut-off frequencies. It is, however, a very limited approach to compare the quality of vision of different species in terms of their behavioral grating acuity, the cut-off frequency for the whole visual system, because the sensitivity of the CNS to spatial frequencies varies throughout the range transmitted. This sensitivity may be expressed as the reciprocal of the threshold contrast which is required for the detection of a given frequency; the whole system is thus best described by the contrast-sensitivity function, CSF, which specifies this value for all transmitted spatial frequencies and was first determined for man by CAMPBELL and ROBSON (1968). More complete specification of the system capability is given when the function is determined over a range of light intensities (VAN NES and BOUMAN, 1967) and orientations (CAMPBELL et al., 1966). Although of interest, the function has not thus far been specified for regions away from the fixation axis.

More recently, CAMPBELL and MAFFEI (1970) have shown that the CSF may be obtained from averaged cortical-evoked potentials in man. This objective technique was subsequently employed to obtain a CSF for the cat (CAMPBELL et al.,

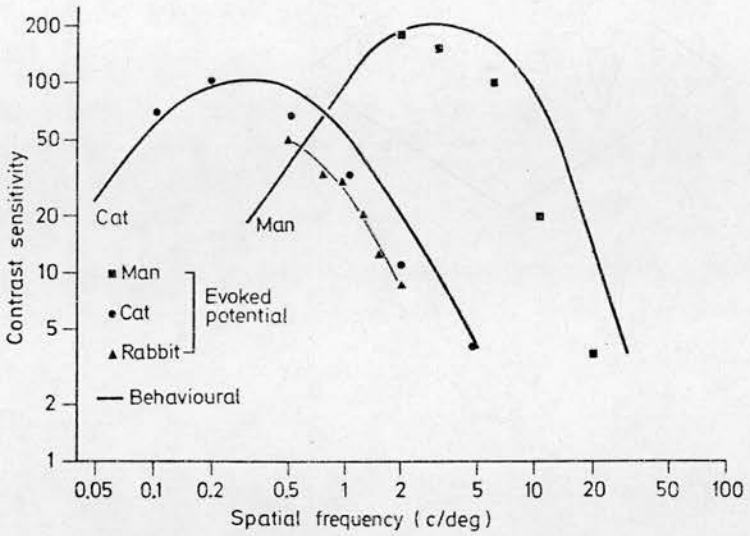

Fig. 26. Behavioral contrast sensitivity functions for man and cat *(bold lines)* compared with functions derived from averaged evoked potentials of man, cat, and rabbit (*square*, *disc*, and *triangle*, respectively). Sources: BISTI and MAFFEI (1974), CAMPBELL et al. (1973), and KULIKOWSKI (1977)

1973) which has now been confirmed by direct behavioral observations (BLAKE et al., 1974; BISTI and MAFFEI, 1974). Behavioral CSF's are also available for macaque (DE VALOIS et al., 1974), squirrel monkey (MERIGAN, 1976), and rabbit (KULIKOWSKI, 1977). The satisfactory cross-species comparison of the CSF ideally requires the function to have been established not only at similar light intensities but also under ecologically characteristic levels of illumination for each form. In the absence of such wide-ranging information, the shape of the available CSF's is similar for all examined species (Fig. 26); it differs from the optical MTF in the possession of a peak sensitivity and a low frequency cut-off. Identified species differences are thus confined to variation in the position of the curve on the frequency axis; the high frequency cut-off of the cat visual system is three octaves lower than that of man and monkey but accompanied by similarly displaced peak sensitivity and low-frequency cut-off. The loss of high-frequency resolution by the cat, relative to the primates, is thus complemented by an extended low-frequency range which is unavailable to man under conditions of continuous photopic viewing. This shift in the position of the CSF on the frequency axis is not determined by the size of the animal, because the squirrel monkey high-frequency cut-off is similar to that of man rather than cat (CAMPBELL et al., 1969; MERIGAN, 1976). CAMPBELL et al. (1973) suggest that the enhanced low-frequency sensitivity of the cat arises because it deals with a closer visual world than man or primates; this seems unlikely in view of the close observation employed by primates during manipulation and their greater range of accommodation than the cat. KIRSCHFELD (1976) has recently argued for relative constancy of the minimum separabile in terms of object space measurement when normalised to body height for a wide

range of forms from insects to large mammals. As a gross approximation this appears to be valid but within the homeotherms alone it is unsatisfactory as suggested above.

The low-frequency reduction in contrast sensitivity which distinguishes the CSF from the MTF of the optic system does not occur under low-illumination intensities (ROBSON and CAMPBELL, 1965) or for short exposure times (SCHOBER and HILZ, 1965; RÖHLER and HILZ, 1966) and is usually accounted for in terms of lateral inhibitory processes (WESTHEIMER, 1972a).

Attempts at explaining visual acuity in terms of retinal morphology and physiology have been of great benefit to the understanding of visual function. The attainment of a similar neurophysiological basis for more complex aspects of visual perception has until recently appeared remote. Now the CSF provides a much more comprehensive description of the visual capabilities of the CNS than does resolution alone, and yet it retains the appearance of tractability to analysis. Its parameters may be established by means of either behavioral studies or objective examination of cortical-evoked potentials. Certain features of the CSF clearly arise during central processing (MAFFEI and CAMPBELL, 1970) and, like its orientation selectivity (CAMPBELL and KULIKOWSKI, 1966), could be explicable in terms of known features of cortical physiology, although the relationship is not as clear-cut as is sometimes made out (BISTI and MAFFEI, 1974).

In principle, a knowledge of the CSF is much more fundamental than it may appear. At threshold, this function defines the spatial-frequency information available to the CNS. Within a limited range, the visual system does appear to operate linearly (CAMPBELL and ROBSON, 1968) so as to enable the prediction of its response to summed spatial-frequency components. Thus, close to threshold, it is possible to describe patterns in terms of their Fourier components and to employ the CSF to set bounds upon the range of patterns the visual system might discriminate. The extent to which a suprathreshold treatment of this nature is justified remains to be established; in this region, however, the system must evince some nonlinearity. The more complex question of whether the visual system actually analyzes its input in terms of spatial-frequency components is beyond the scope of this work but has been discussed in some detail (CAMPBELL, 1974; ROBSON, 1975). Recent results (HENNING, HERTZ and BROADBENT, 1975) are inconsistent with the hypothesis that the visual system analyses spatial patterns in independent, narrowly tuned bands of spatial frequency.

F. Conclusion

Taxonomists are generally characterized as "splitters" or "lumpers" according to the readiness with which they subdivide the living kingdom; the history of comparative visual physiology suggests it to be more inbued with the spirit of the former. This "set" for the discovery of contrast between species has often led to

the establishment of artificial dichotomies on the basis of preliminary results and a consequent premature emphasis on explanatory theorizing. No species of mammal has so often been set apart on the basis of visual physiology as the rabbit, which is normally taken as representative of lateral-eyed mammals in general. Undoubtedly the most obvious organizational feature of a given visual system is its relative exploitation of the frontal and lateral fields of view, and it is natural to anticipate the possibility of equally overt contrasts in the organisation of the CNS which are consequent upon the disposition of the eyes. The extreme laterality of the rabbit eye thus appears to predispose to the acceptance of results indicating its qualitative difference from the cat, monkey, and man, whereas distinctions between the latter species tend to be underemphasised.

Several early investigators reported that the rabbit, in contrast to other mammalian species, did not show optokinetic nystagmus (URBANTSCHITSCH, 1910; BARTELS, 1920), but subsequent technical improvements (TER BRAAK, 1963; BRECHER, 1936) enabled its ready demonstration, and now it is regarded to play a greater role in rabbit eye movements than in most other mammals (HUGHES, 1971). Associated with the extreme stability of the rabbit eye, which arises from its powerful optokinetic mechanism (COLLEWIJN, 1971), is the often-claimed absence of spontaneous eye movements. BRECHER (1936) regarded the role of the rabbit's eyes as *Warnorgane* to be so preeminent as to be consistent with the absence of voluntary eye movements. This view, supported by the great extent of the animal's visual streak, has been long accepted and regarded as qualitatively distinguishing the rabbit from other mammalian species. Nevertheless, spontaneous eye movements are readily visible in the rabbit (HUGHES, 1971; COLLEWIJN, 1977), even vergence is now reported (COLLEWIJN and ZUIDAM, 1977); it remains true that these movements are much less frequent than in man or cat (PRITCHARD and HERON, 1960; WINTERSON and ROBINSON, 1975; STRYKER and BLAKEMORE, 1972), and monkey (FUCHS, 1967). It appears, however, that the rabbit does not follow small objects with smooth tracking as do cat, dog, and monkey (RADEMAKER and TER BRAAK, 1948). The *Willkürliche Fixation* described for the rabbit by FLEISCH (1922) was shown to be a special instance of optokinetic nystagmus (BRECHER, 1936). Certainly the extent of the visual field and area centralis would be expected to quantitatively influence the patterns of eye and head movements in different species, but the available evidence does not support extensive qualitative distinctions between mammalian species.

Of course it remains possible that there are substantial differences in the neuronal organization of mammalian forms, but again caution is recommended in classification. Some years ago, when it was believed that mammalian retinal ganglion cells possessed only concentric receptive fields, MATURANA (1964) discriminated between an indeterminate mammalian visual system, characteristic of animals possessing neocortex to which nonspecific information is supplied and deterministic systems in amphibians, reptiles, and birds which lack neocortex and whose retinal output is specialized and unambiguous. The report of nonconcentric units in the rabbit (BARLOW et al., 1964) caused this concept to give way to that of a spectrum of animals in which the rabbit fell between the highly encephalized species, such as monkey and cat, whose retinas were equipped only with concentric units and the forms, such as reptiles and birds, which lack neocortex

and possess complex retinas. It has been suggested (HUGHES, 1971) that peripheral preprocessing by nonconcentric units is required in the rabbit in order to reduce the enormous demands on cortical area which would occur if its visual-streak projection were analysed in similar fashion to those of the smaller cat area centralis.

The subsequent discovery of substantial nonconcentric retinal unit populations in cat and other mammalian species has substituted quantitative for these qualitative distinctions. Reference to current observations of higher levels of the visual system might again enable qualitative distinctions to be established. Although the cat LGN (WILSON and STONE, 1975; CLELAND et al., 1975) is now known to receive the projections of some nonconcentric units, as does that of the rabbit (OYSTER et al., 1971), the rabbit visual cortex is described by many authors to be very different from that of cat and monkey (OGAWA et al., 1968; HUGHES, 1971; VAN SLUYTERS and STEWART, 1974a). The situation outlined above in relation to the retina should, however, serve as a warning against too readily emphasizing distinctions based upon encounter rates in single-unit populations.

Nevertheless, we continue to find the size of the lateral and binocular fields of the rabbit implicated in accounting for all manner of observations discrepant with findings in the cat. Thus, rabbit monocular and binocular cortical units (CHOW and SPEAR, 1974; VAN SLUYTERS and STEWART, 1974b) are described as unhindered by deprivation during development or by selective experience (MIZE and MURPHY, 1973); a great contrast with the situation in the cat. BLAKEMORE and VAN SLUYTERS (1975) accept this negative evidence and set out to account for the discrepancy between the two species. In view of the substantial discrepancies which exist in this field between the findings of those working on *one* species (e.g., HUBEL and WIESEL, 1963; BARLOW and PETTIGREW, 1971; BUISSERT and IMBERT, 1976), it might be argued that such an attempt is very premature. BLAKEMORE and VAN SLUYTERS (1975) suggest that plasticity such as found in the cat enables matching of binocular receptive field properties in the two eyes, a condition perhaps necessary only for highly binocular species. They emphasise the panoramic nature of rabbit vision and the bizarre features of some of its binocular units. The presence of a proportion of binocular fields which are capable of subserving stereopsis in the rabbit is ignored, in spite of the fact that these units might equally require plasticity for "matching" of their left and right eye contributions, regardless of the animal's binocular field width. The traditional predisposition to differentiate the lateral-eyed species thus tends to override the available evidence, but even such distinctions as appear well founded should not be generalized before demonstration of their applicability to lateral-eyed species other than the rabbit.

The tendency to turn quantitative distinctions between species into qualitative distinctions is, perhaps, no more evident than in discussions of visual acuity. The investigator only mildly afflicted with anthropomorphism describes the low acuity of the rat as 'poor acuity' but a more serious condition manifests itself in compound ignorance by the suggestion that 'rats are as blind as bats.' We would do well to remember Sir THOMAS BROWNE's dictum (1658; 1912),

'if the Eagle were judge, we might be blind ourselves.'

G. Acknowledgments

My debt to regular and transient devotees of Professor P. O. BISHOP's lunch table for their stimulating, critical, and sometimes tedious observations on topics dealt with above has already been pointed out to me by some of them, but I here give formal recognition of my gratitude.

I am greatly indebted to LYN SPEIGHT for her extensive assistance during the preparation of this chapter.

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OPTICS

SCHEMATIC EYES

Vision Research Vol. 19, pp. 569 to 588
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0042-6989/79/0501-0569$02.00/0

A SCHEMATIC EYE FOR THE RAT

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(*Received* 17 *July* 1974; *in revised form* 11 *September* 1978)

Abstract—Previously published rat schematic eyes are shown to be inadequate and a new one is developed. It is demonstrated that a homogeneous lens is not satisfactory for modelling a small eye and a core lens model is provided. Attention is paid to the estimation of the confidence limits of the refractive state derived from the schematic eye computations. Other sections deal with peripheral aberrations, posterior nodal distance, exit and entrance pupils and the extent of the uniocular and binocular theoretical and observed visual fields of the rat.

INTRODUCTION

Massof and Chang (1972) have criticised Block's rat schematic eye (1969) because the *measured* refractive index of the rat lens does not attain the value of 1.61 used in Block's calculation but ranges from 1.39 at the capsule to 1.5 at the core (Phillipson, 1968). They conclude that the power of Block's schematic lens is excessive and provide a new model eye based upon Phillipson's results. Massof and Chang thus fail to realise that the value of 1.61 is an "effective" or "total" refractive index (Gullstrand, 1925; Vakkur and Bishop, 1963; Block, 1969; Hughes, 1972)—a fiction which enables a homogeneous lens of the same dimensions as the real one to be calculated while neglecting the gradients of refractive index in the crystalline lens. The use of a mean index which is arbitrarily derived from measurements on the lens (Massof and Chang, 1972) is totally inadequate; it leads to a deficit in lens power of some 130D which is readily detected by following Block's procedure of comparing the calculated with the experimentally determined lens back vertex power.

Although Block's schematic rat eye is internally consistent and pragmatically justified by his results, there remain several justifications for the recomputation of a rat schematic eye from fresh data:

(a) Block made no attempt to measure the axial length of the eye directly but deduced it from the results of retinoscopy so that his computations cannot contribute to the discussion concerning the refractive state of the eye.

(b) A previous paper (Hughes, 1977a) has demonstrated Block's conclusion that the rat eye is 10 D hypermetropic at the receptor plane to be false under photopic conditions.

(c) The axial length, lens thickness and lens surface curvature of Block's model eye are all extraordinarily small when compared with those in the tables of Lashley (1932), Hermann (1958) or measured in this laboratory on animals of even half the age quoted by him.

(d) As demonstrated subsequently, the homogeneous lens model used by Block is unsatisfactory for small eyes and is better replaced by a core lens.

METHODS

Fourteen rats of the D.A. strain, ranging from 115 to 130 days of age, were anaesthetised by intraperitoneal injection of 1 cm^3 of 25% urethane solution.

It is customary to carry out many of the measurements necessary for the computation of a schematic eye on an enucleated eye whose internal pressure is maintained by using a hypodermic needle to connect the globe with a hydrostatic pressure reservoir. This is not satisfactory for small eyes because there is a great risk of distorting the globe or displacing the lens; it will be seen later that the schematic eye parameters of small eyes are susceptible to very slight departures of the tissues from their normal dimensions. Photography of the enucleated eye without connection to a pressure reservoir was thus investigated by comparing the dimensions determined from photographs of a living eye whose blood supply was intact with those established from a swiftly ligatured and enucleated eye.

The following procedure was adopted for the three animals used in the comparison of the techniques. The rat was equipped with a long tracheal cannula. Both eyes were dissected free from all connections other than the optic nerve and its associated vessels; the posterior pole was cleaned of muscle so that it would be well defined in the subsequent photographs. The head and eyes were then immersed in saline while the rat continued to breath through the cannula which reached above the surface of the liquid. Movements of the saline surface induced by breathing were minimised by holding the body up with a clamp. In saline the corneal power is almost eliminated so that a single photograph showing the corneal vertex, lens vertex and posterior pole of the globe could be taken with an Asahi Pentax Spotmatic 500 camera fitted to a Zeiss Ikon Dissecting Microscope. The limited depth of field of this arrangement facilitated the orientation of the plane of photography to give an equatorial optical "section" for the measurement of dimensions. The orbital fat was replaced by cotton wool pads upon which the globe was oriented with the pupil plane vertical before photography.

A scale aligned with the most important axis of measurement was included in each photograph; two further scales parallel and perpendicular to the original were included when making the prints upon which measurements were made, and enabled correction for the dimensional instability of the printing paper. The prints of these and subsequent photographs were enlarged thirty-five times. It was thus possible to determine the following dimensions from this first photograph (each as the mean of three estimates

based on the random conjunction of the scale of a steel rule with dividers set from the photograph):

(a) Corneal apex to lens apex
(b) The axial length of the eye
(c) The radius of curvature of the anterior corneal surface
(d) The radius of curvature of the lens anterior surface.

The scale could be read to about ± 0.25 mm, thus giving the dimensions of the eye within $\pm 0.25/35 = 0.007$ mm. The head was subsequently raised from the bath of saline and the scleral image of a distant slit of known dimensions and distance was photographed while the circulation of the eye remained intact. Prints of these photographs, and similar ones made with enucleated eyes, were subsequently used to estimate the posterior nodal distance.

A ligature was then passed round the optic nerve and vessels of the same eye which was enucleated and swiftly transferred to a saline bath where a second photograph was made for comparison with that of the eye *in vivo*. This photograph was printed and analysed in exactly the same fashion as the previous one.

Comparison of the results from the two methods revealed no significant difference for the three animals so that the subsequent data was obtained in the simplest fashion by photographing rapidly ligatured and enucleated eyes. The mean of the successful measurements of each parameter was computed and tabulated for use in the schematic eye calculation which thus represents an average eye. Several individual schematic eyes were also computed and found to have parameters of similar magnitude to those of the average eye. These individual results have not been included.

The eye was opened around the corneoscleral junction, the lens extracted, cleared of vitreous, and photographed in dorsal view while standing upright in a saline bath. A scale was included in the bath at the focal plane which enabled the subsequent measurement of its (a) anterior radius of curvature; (b) posterior radius of curvature; (c) axial length; and (d) diameter.

Samples of cornea, retina and sclera were taken near the optic axis and cut on a freezing microtome to give radial sections whose thickness was subsequently measured at $\times 100$ when immersed in saline.

The back vertex power of the lens was measured in a trough with optically flat glass walls which was fitted to a microscope moving stage so that it could be shifted back and forth along a beam of light vergent to 10 m and passing directly under the objective. A micrometer dial gauge enabled the stage position to be read to an accuracy of about ± 0.0025 mm. The trough was filled with a solution of fluorescein in saline and the lens placed upright in a depression at the top of a small pillar, which stood in the trough and was centred in the light beam. A 2 mm artificial pupil was placed in front of the lens. The centre of the eyepiece graticule was aligned with the posterior vertex of the lens and the micrometer reading of the stage position taken. The lens was moved along the light beam until the graticule was aligned with the region of minimum confusion in the beam emergent from the lens, the beam was readily visible in the fluorescein solution, and the micrometer read again. The mean of 6 differences between the two micrometer readings was taken for the purpose of calculation, but the region of minimum confusion of the emergent beam appeared quite extensive and it is concluded that its centre could not be estimated closer than about ± 0.03 mm under these conditions of measurement. The small amount of entrance beam vergence was neglected in this measure of the back vertex distance of the lens. The measurements were carried out in saline rather than air (Block, 1969) to increase the distance involved and thus their accuracy. The inverse of the back vertex distance in meters is taken as the back vertex power of the lens and is expressed in diopters.

The capsule of the lens was gently removed by finger pressure and samples of the outer and inner cortex taken. The core was cleaned and photographed for the determination of its dimensions, after which a sample was taken from its centre. These lens samples, along with others of cornea, aqueous humour and vitreous humour, were examined with an Abbé refractometer by means of which their refractive index was determined.

After the optic nerve and vessels of the second eye had been ligatured and cut it was immediately transferred to a freezing microtome fitted with a Pelcool device. The eye was orientated on the platform to give a section through the vertical meridian of the globe. Cutting continued until half the measured width of the globe had been removed. The surface thus revealed was wiped over to remove ice crystals and photographed to give a second set of dimensions for comparison with the *in vivo* measurements. The surface of the sectioned lens revealed the core boundary as a rather darker region and thus gave measurements for comparison with the dissected lens.

False apparent position of the lens

The refractive index of the rat cornea, 1.38, is slightly greater than that of saline, 1.336, so that, when the eye is immersed in saline and viewed perpendicular to the optic axis, the lens vertex appears to be slightly forward of its real position. The reason for this is readily understood by reference to Fig. 1, which diagrams the path in the vertical meridian of a ray starting off tangent to the front vertex of the lens. For simplicity the corneal margins are assumed to be concentric; the angle of refraction of the beam was measured directly on a photograph and found

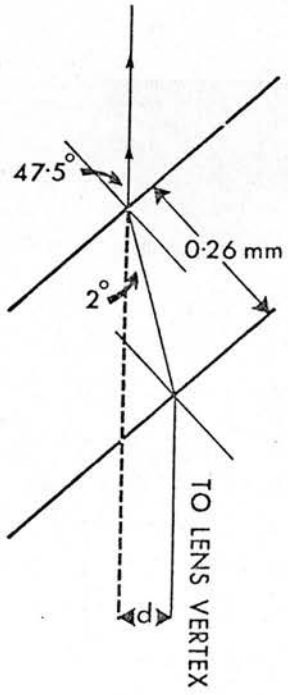

Fig. 1. A vertical section through the upper cornea showing the forward displacement, d, during corneal refraction of a ray which originates tangent to the lens vertex. The angle of refraction of the emergent ray, 47.5°, was estimated directly from a photograph; the derivation of text equations 1 and 2 follows from inspection.

to be 47.5° in the appropriate region of the cornea. Given the thickness of the cornea (t), then the apparent forward displacement of the lens vertex (d) is seen by inspection to be

$$d = \frac{t \operatorname{arc}(i - r)}{\cos r} \quad (1)$$

where

$$r = \sin^{-1}\left(\frac{1.336}{1.38}\sin i\right) \quad (2)$$

$$d = 0.013\text{mm}.$$

This correction has been added to all of the measurements of the separation of the corneal and lens vertices in the table of results.

THE RAT SCHEMATIC EYE

Conventions and data

The mean values of the measurements described in the previous section are summarized in Table 1. The contents of Table 1 are used for the calculation of an average rat schematic eye subsequent to which the significance to be attached to the computed schematic eye parameters is discussed in the light of the tabulated standard errors and estimated errors of measurement.

Calculation of the schematic eye begins with the use of thick lens theory to develop an equivalent lens for the cornea and for the crystalline lens. The calculation is completed when a further thick lens is derived to represent the behaviour of the whole eye by the combination of the equivalent corneal and crystalline lenses. This model is valid for axial rays alone.

The following conventions are observed in the calculations. Light rays enter the system from left to right; the refractive indices of the media encountered are numbered in the same direction beginning with air, n_1; surfaces are numbered in the order encountered beginning with the anterior vertex of the cornea, A_1, which is used as a reference point for the measurement of distances. Measurements from a given point to its right are positive. Surfaces convex to the light are defined as having positive radii of curvature, r. The first principal point of a system is indicated by a suffixed capital letter, e.g. H_{12}, but the second principal point is prime, H'_{12}.

The necessary calculations were carried out according to the schedule of Southall (1933) as previously illustrated for the rabbit (Hughes, 1972). Six decimal places were used during the computations in order to obtain a consistent system but *the published results have been rounded off to three places of decimals.* This degree of accuracy of measurement is not implied.

The homogeneous lens and its inadequacy

The gradient of refractive index through the crystalline lens makes the straightforward application of the simple lens formula inappropriate. One solution is to dispose of the refractive index measurements and to represent the lens by an equivalent organ of identical shape but of uniform and higher refractive index; this is the *homogeneous lens model* which was used by Vakkur and Bishop (1963) for the cat, by Hughes (1972) for the rabbit, and both Block (1969) and Massof and Chang (1972) for their rat schematic eyes. The parameters of the homogeneous lens model and a schematic eye based on it are provided in Table 2.

Table 1. Measurements for the schematic eye of the rat

	Mean	Average eye S.E.M.	No.	Accuracy ± mm
Strain	D.A.		14	
Age (days)	125	—	14	—
Eye length (mm)	6.29	0.04	14	0.007
Eye width N.T. (mm)	6.41	0.063	7	0.007
Cornea height (mm)	2.11	0.01	7	0.007
Cornea thickness (mm)	0.26	0.002	6	—
Cornea Vx—lens Vx (mm)	0.88	0.02	9	0.007
Cornea surface radius (mm)	2.97	0.026	15	0.007
Cornea base radius (mm)	2.82	0.027	7	0.007
Cornea refractive index	1.38			
Aqueous refractive index	1.337			
Lens thickness (mm)	3.71	0.05	15	0.007
Lens diameter (mm)	4.23	0.077	9	0.007
Lens radius front, Lens radius rear } Av. (mm)	2.34	0.03	12	0.007
Lens core radius (mm)	1.0	—	4	—
Capsule refr. index	1.39			
Core refr. index	1.50			
Back vertex dist. (mm)	3.64	0.045	8	0.03
Vitreous refr. index	1.337			
Retina thickness (mm)	0.17	0.002	6	—
Choroid and scleral th. (mm)	0.14	0.002	6	—
P.N.D. (mm)	3.39	0.03	6	—
Curvature post. scle. (mm)	3.23	0.022	10	0.007

The homogeneous lens may be calculated to replicate the back vertex distance of the real lens within the error of measurement, but its principal points are necessarily separated by a greater interval than those of the crystalline lens, and its refractive power is greater (Helmholtz, 1909, p. 99–104; Gullstrand, 1925, p. 349). The misrepresentation of the principal points of the whole eye resulting from the use of a homogeneous lens as a model for the cat crystalline lens is small—amounting to only 0.5 D (Vakkur and Bishop, 1963)—so that more complex models have not previously been employed, but this is not an acceptable course for the small eye of the rat because the consequent error may amount to more than 4 D.

Design of the two shell lens model

An alternative for the homogeneous lens model has only been presented in the form of the core model lens of the human schematic eye (Gullstrand, 1925). The centre of all but the most youthful human lenses can be differentiated as a "core" region somewhat denser than the surrounding "cortex". In the core lens model, the lens system is composed of four refracting surfaces. The first two surfaces form the anterior cortex and the second two form the posterior cortex. The equivalent core lens is situated between the second and third surfaces and is regarded as a lens of the same refractive index as that at the centre of the crystalline lens and suspended in a medium of the same refractive index as that of the crystalline lens vertices.

The dimensions of the equivalent core lens were obtained in the human schematic eye by the solution of the indicial equation for a meridional section through the optic axis of the lens after the necessary constants had been established. Amongst the latter is the refractive power of the crystalline lens which was determined from observations made on the aphakic human eye; knowledge of this factor uniquely specifies the core dimensions and establishes the location of the principal points of the core lens model at the position corresponding to that in the crystalline lens. The equivalent core lens is thus determined by calculation and not by anatomical observations—it has no exact physical equivalent.

By contrast, we at present have no information from aphakic rat eyes and no knowledge of the refractive power of the crystalline lens. The set of unknowns entering into the computation is thus larger; if other variables are kept constant then for a given core shape, i.e. radius of curvature and position, there is a unique combination of principal point position and lens refractive power which replicates the measured back vertex distance of the original crystalline lens. Without knowledge of the refractive power we cannot develop the necessary core dimensions and uniquely locate the principal points of the equivalent core lens at their positions in the real lens. A vast number of solutions exist which give principal point positions between conjunction and the separation found in the homogeneous lens solution, which is the upper limit. If a specific core shape can be justified then a unique solution may be obtained.

An approximate solution may, however, be developed. The crystalline lens of the rat contains a solid core which is of high refractive index relative to the capsule and may be extracted from the semi-liquid cortex by means of a gentle squeeze. The lens core proves to be almost spherical in section, 2.0–2.3 mm thick along its antero-posterior axial dimension and with a major to minor axis ratio of between 1:1 and 1.15:1. A section made perpendicular to the equator of a lens mounted on a freezing microtome reveals the boundary of the core as a darker circular band of radius about 1–1.2 mm in the lens matrix. This conclusion was strikingly borne out by the data of Phillipson (1969) which includes the equatorial and anteroposterior distributions of protein concentration in a lens of 220 days of age; this differs little from that of the 130-day-old lenses employed in this study and may be accepted as characteristic of them. The distributions were replotted in terms of refractive index as shown in Fig. 2a and b. The physical transition from the semi-liquid cortex to the solid core was identified by Phillipson as corresponding with the region at which the refractive index reached a value of 1.45.

With this information it is possible to approximate the isoindicial curves. We consider the lens in meridional cross section—assuming its properties to be invariant with rotation about the optic axis—and plo. the four specified points of refractive index 1.39, 1.42 and 1.45. For each half of the lens we assume the

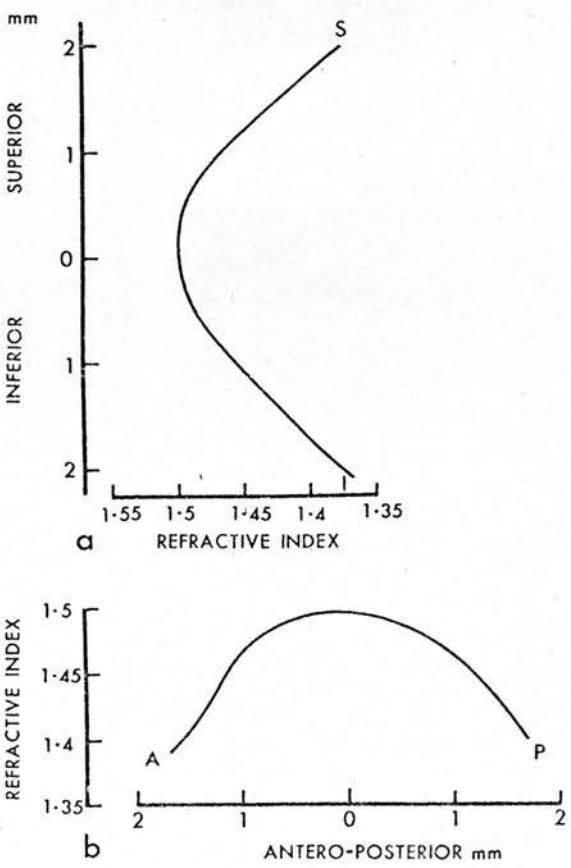

Fig. 2. Phillipson's (1969) refractive index determinations are here shown along a vertical diameter passing through the equatorial plane and along the antero-posterior axis of the rat lens.

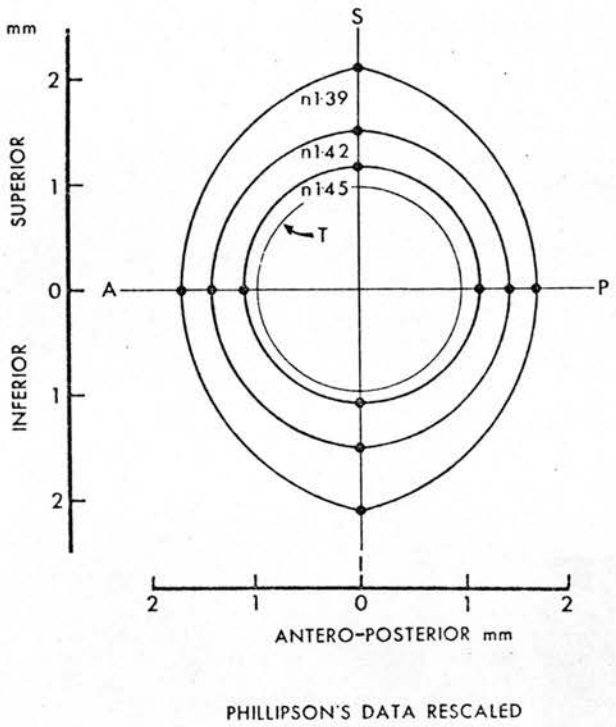

Fig. 3. Phillipson's refractive index estimates (1969) are displayed as filled circles at the sampled position on a vertical section containing the antero-posterior axis of a revolution of the lens. For each half of the lens it has been assumed that the isoindicial curves are described by the circle whose radius of curvature and centre is uniquely defined by the three relevant samples. The 1.39 isoindicial curve matches the lens capsule in form and the 1.45 curve is a circle which is closely approximated by the theoretical core, *T*, of the core lens model developed in the text.

isoindicial curves to be fitted by a circle whose radius of curvature is uniquely determined by three of the plotted points. The rat lens is symmetrical about its equatorial plane and when the selected isoindicial curves are drawn (Fig. 3) it is found that the boundary formed by the 1.39 value of refractive index closely matches the form of the lens capsule and is biconvex, whereas the core, defined by the 1.45 isoindicial curve, is circular and of radius 1.1 mm. Its shape corresponds admirably with that suggested by the physical core.

If a two shell or core model lens is calculated on the assumption of a spherical core 1 mm in diameter, a refractive index of 1.39 for the cortex, 1.5 for the core and the measured anterior and posterior lens radii of curvature, then the back vertex power is found to be within 2% of the average value for the crystalline lens. Successive approximation enables a perfect correspondence to be obtained when the core radius is set at 0.958 mm. This value is slightly smaller than the 1.0–1.1 mm suggested by direct measurement but there is good reason for the discrepancy. The *spherical* form of the core, its refractive index and that of the cortex having been selected, then the radius of curvature of the core is lost as an independent variable and only the core radius can be adjusted to compensate for the absence of the gradient of refractive index in the schematic lens. For a given back vertex power the solution obtained is unique. The parameters of this model lens and the schematic eye computed from it are presented in Table 2. Computation of the two shell lens follows the schedule of Southall (1933).

The core model lens established in the fashion described above cannot be relied upon to have its principal points at the *same* position as those of the crystalline lens which it represents. Although the core of the rat schematic lens is a mathematical fiction, just as in the human schematic eye, it is very similar in its properties to the real core and it can be concluded that the principal points will be less erroneously positioned than is the case for the homogeneous lens model. This discrepancy between the real and core lens remains an unassessed influence on the refractive state of the final computed schematic eye and is quite independent of measurement errors and population variation.

A diagrammatic cross section of the two shell or core lens, schematic eye for the rat is presented in Fig. 4, accompanied by photographs of the eye and lens in photomontage and frozen section in Fig. 5.

THE REFRACTIVE STATE OF THE RAT SCHEMATIC EYE

Mean refraction

Specification of the refractive state of the rat schematic eye necessitates the choice of some surface in

Table 2. The rat average schematic eye

Index of refraction		
Cornea	n_2	1.380
Aqueous and vitreous	n_3 & n_7	1.337
Lens cortex	n_4 & n_6	1.390
Equivalent core lens	n_5	1.500
Homogeneous lens (total)	n_1	1.683
Retina	n_8	1.351

Position		
Anterior cornea surface	A_1	0.000 mm
Posterior cornea surface	A_2	0.260 mm
Anterior lens surface	A_3	0.881 mm
Anterior core surface	A_4	1.778 mm
Posterior core surface	A_5	3.695 mm
Posterior lens surface	A_6	4.591 mm
Retina surface	A_7	5.981 mm
Outer limiting membrane	A_8	6.111 mm
Choroid/retina interface	A_9	6.151 mm
Posterior scleral surface	A_{10}	6.291 mm
Outer limiting membrane emmetropic (core model)	A'_8	6.178 mm
Posterior scleral surface for emmetropia (core model)	A'_{10}	6.357 mm

Radius	
Anterior cornea surface	2.965 mm
Posterior cornea surface	2.705 mm
Anterior lens surface	2.340 mm
Anterior core surface	0.958 mm
Posterior core surface	0.958 mm
Posterior lens surface	2.340 mm

Schematic cornea		
Cornea anterior surface power	F_1	128.162D
Cornea posterior surface power	F_2	−15.896D
Cornea total power	F_{12}	112.649D
Cornea first principal point	A_1H_{12}	−0.026 mm
Cornea second principal point	$A_1H'_{12}$	−0.28 mm

Schematic core model lens		
Lens anterior surface power	F_3	22.650 D
Lens anterior core power	F_4	114.781 D
Lens posterior core power	F_5	114.781 D
Lens posterior surface power	F_6	22.650 D
Lens anterior cortex power	F_{34}	135.753 D
Lens posterior cortex power	F_{56}	135.753 D
Lens total power	F_{36}	243.991 D
Anterior cortex first principal point	A_3H_{34}	0.729 mm
Anterior cortex second principal point	$A_4H'_{34}$	−0.161 mm
Posterior cortex first principal point	A_5H_{56}	0.161 mm

Schematic homogeneous lens		
Lens anterior surface power	F_3	147.889 D
Lens posterior surface power	F_6	147.889 D
Lens total power	F_{36}	247.567 D
Lens system first principal point	A_3H_{36}	1.761 mm
Lens system second principal point	$A_6H'_{36}$	−1.761 mm
Lens system posterior focal length	$H'_{36}P'_2$	5.401 mm
Lens system back vertex distance	$A_6P'_2$	3.640 mm

Average schematic eye (core lens)		
Eye total power	F	300.705 D
Eye first principal point	$H_{12}H$	1.651 mm
Eye second principal point	$H'_{36}H'$	−1.019 mm
Eye anterior focal length	HP	−3.326 mm
Eye posterior focal length	$H'P'$	4.446 mm
Anterior nodal point	A_1N	−2.771 mm
Posterior nodal point	A_1N'	2.852 mm
Out of focus distance	A_8P'	0.067 mm
Posterior nodal distance	$N'P'$	3.326 mm
Refractive state	K	4.616 D
Emmetropic model axial length	$A_1A'_{10}$	6.357 mm
Retinal magnification factor	RMF	0.059 mm
Posterior cortex second principal point	$A_6H'_{56}$	−0.729 mm
Lens system first principal point	$H_{34}H_{36}$	1.111 mm
Lens system second principal point	$H'_{56}H'_{36}$	−1.111 mm
Lens system posterior focal length	$H'_{36}P'_2$	5.480 mm
Lens system back vertex distance	$A_6P'_2$	3.640 mm

Average schematic eye (homogeneous lens) (not used because of large systematic error)		
Eye total power	F	305.116 D
Eye first principal point	$H_{12}H$	1.603 mm
Eye second principal point	$H'_{36}H'$	−0.975 mm
Eye anterior focal length	HP	−3.277 mm
Eye posterior focal length	$H'P'$	4.382 mm
Anterior nodal point	A_1N	2.708 mm
Posterior nodal point	A_1N'	2.960 mm
Out of focus distance	A_8P'	0.125 mm
Posterior nodal distance	$N'P'$	3.277 mm
Refractive state	K	9.03 D

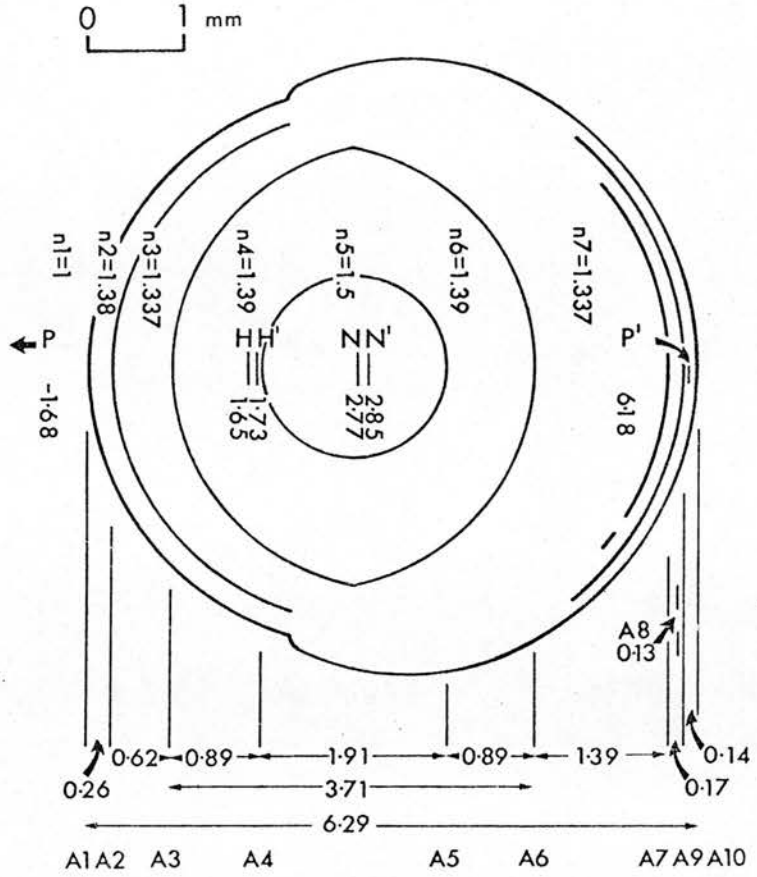

Fig. 4. The main parameters of the rat schematic eye in diagrammatic form. Measurements are given in millimetres from the corneal vertex or between the points indicated by arrows. The refractive index of the various media is indicated by the letter n bearing a suffix. Comparison of this eye with that of the rabbit and cat emphasises the relatively large volume of the lens and thickness of the retina in the rat.

the retina to be that at which the given image plane is brought to a focus in the conscious animal. This has been described as the "effective image shell" (Hughes, 1977b) and located at the plane of the photoreceptor entrance apertures (Hughes, 1977a, p. 936), i.e. the outer limiting membrane. In the rat this plane is set 40 μm vitread of the retina/choroid junction (Lashley, 1932) and its distance, d, from the corneal vertex may be obtained from Table 2. The refractive state of the various model eyes, K, is computed by means of the relationship:

$$K = \frac{n_7}{d - A_1H'} - F. \qquad (3)$$

Thus we obtain the results given in Table 3.

The eyes computed from average measurements are thus both hypermetropic, with the homogeneous-lens model some 4.4 D more ametropic than the core model. On theoretical grounds alone we may be confident that the core model approximates the living eye more closely than the homogeneous lens model because of the inevitably smaller separation of the principle points of its lens (Table 3). The homogeneous lens model is thus neglected in subsequent discussion.

Error of measurement and sampling. It has not been customary to assess the accuracy of schematic eye derivations for large eyes, such as those of rabbit and cat, because accuracy of measurement is high relative to the magnitude of error which would significantly influence the refractive state of the model. However, for small eyes, such as those of the rat, some analysis of error is necessary to establish the confidence to be put upon the computed refraction.

Table 2 includes an estimate of the maximum error of measurement of each parameter. These errors have been compounded in the usual fashion (Braddick, 1966) throughout the computational schedule of the schematic eye in order to assess the range of error in computed refraction which could be encountered. The error of measurement of the back vertex distance of the crystalline lens was attributed to the core radius because the latter is the only independent variable during the relaxation procedure of computing the model lens. The refractive state of an individual schematic eye was thus found to be specified within a *range* of ± 5.3 D. A large number of such compu-

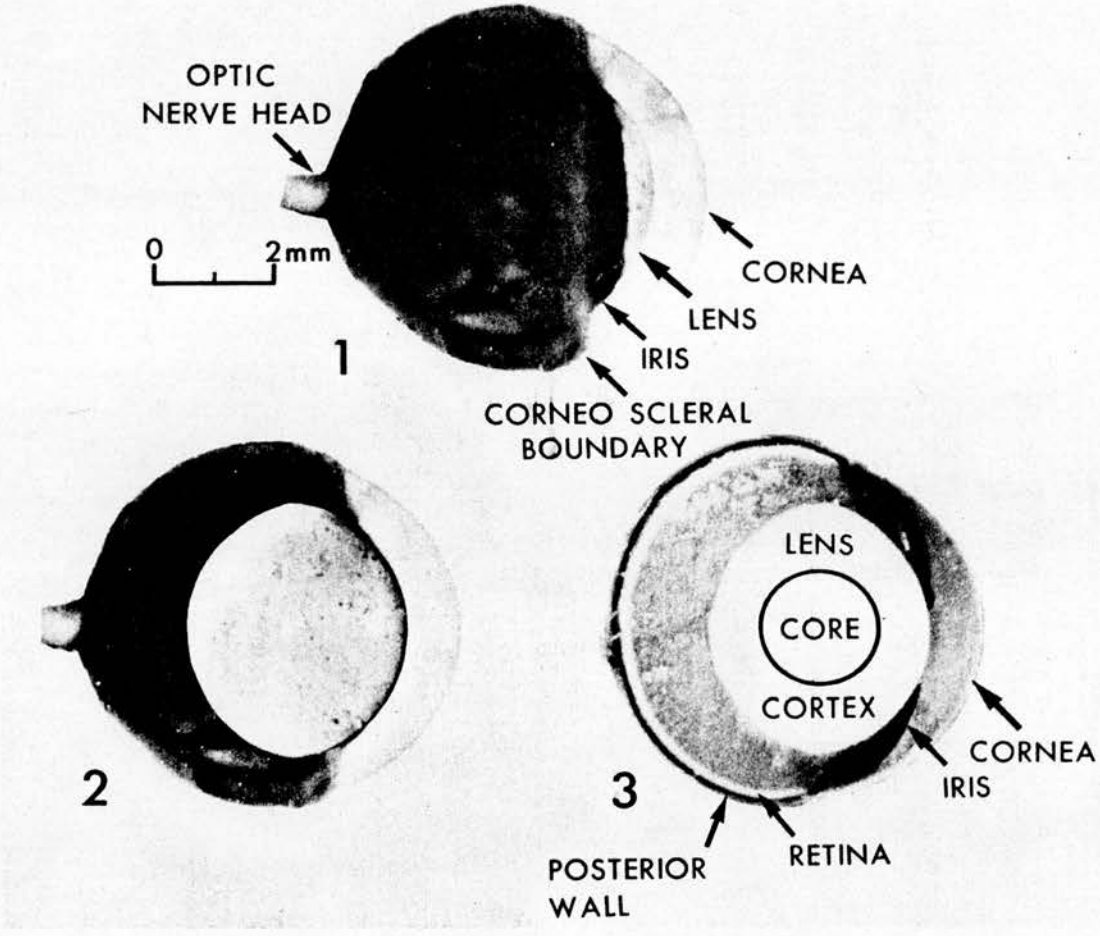

Fig. 5. *1.* The rat eye photographed in dorsal view under saline to reveal the relative positions of the cornea and lens. *2.* Photomontage in which a photograph of the extracted lens of the eye in dorsal view is shown in its correct position. *3.* Frozen horizontal section of the rat eye in dorsal view cut at a plane just above the optic nerve head. The lens core may just be made out in the original but for reproduction it has been emphasised by a fitted circle. Compare this photograph with the diagram of Fig. 4.

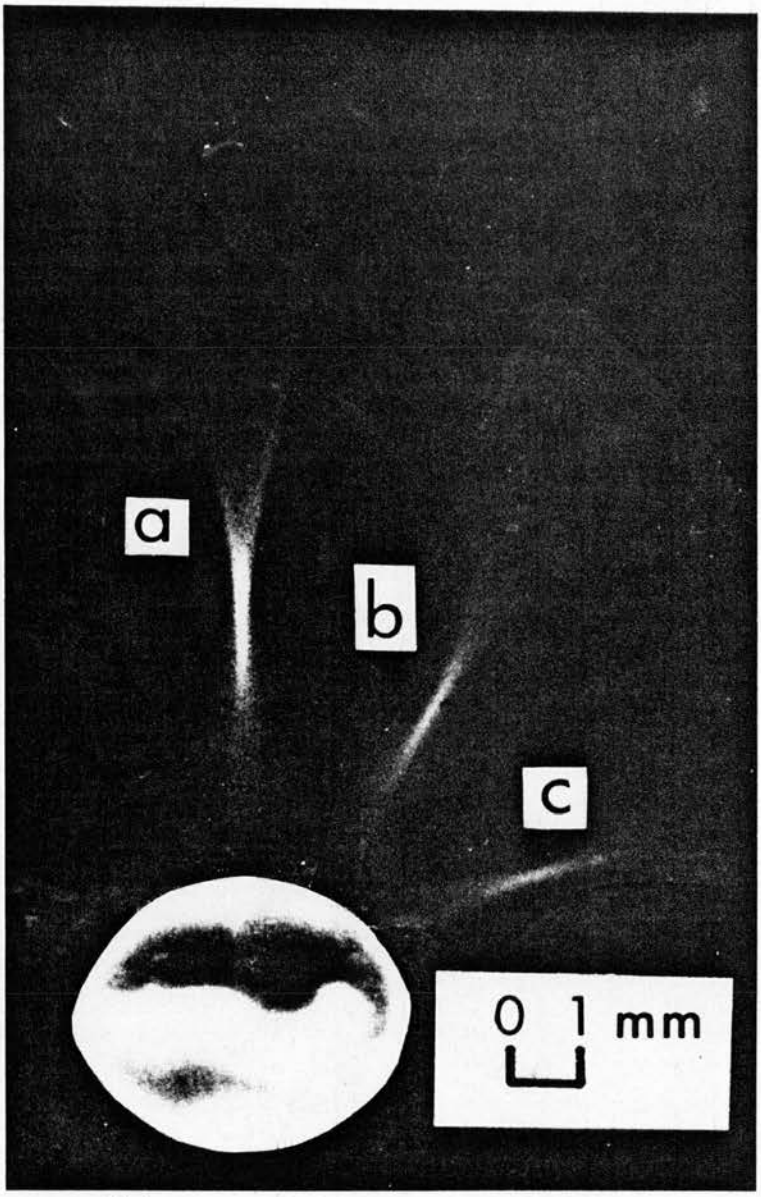

Fig. 7. Photograph of light rays emerging from a rat lens which is immersed in a fluorescein saline solution. Beam *a* results from the refraction of a parallel beam entering the lens along the optic axis, *b* from a beam entering 30° oblique to the optic axis, and *c* from rays 75° oblique to the optic axis. The form of the caustic curve and position of the circle of least confusion is readily seen in the emergent rays of *a*. The axial cusp pointing towards the lens reveals negative aberration in *a* and *b* but in *c* there is a suggestion of positive aberration. The power of the lens appears to increase for the more oblique rays.

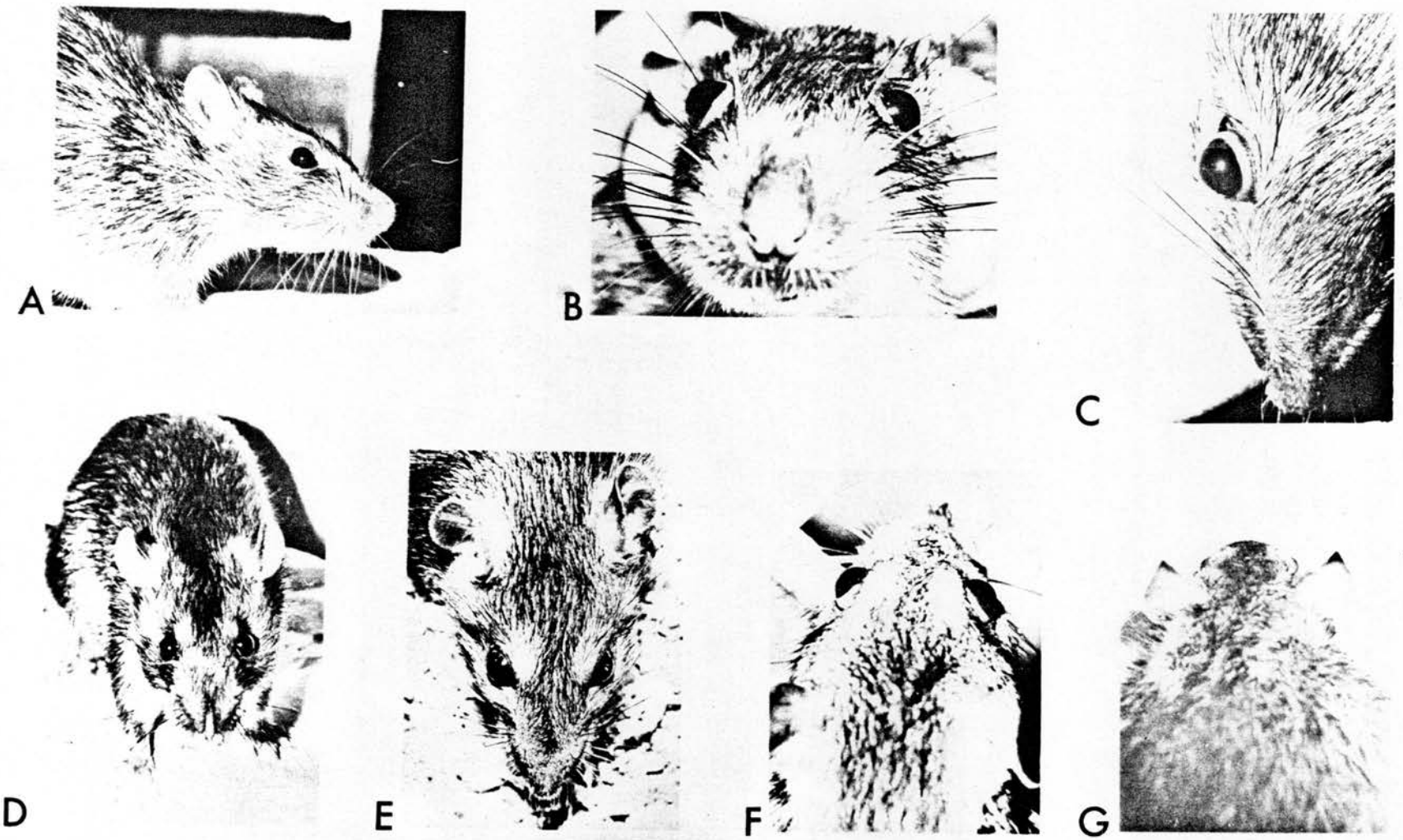

Fig. 13. Views of the rat head and eyes. A. The head in lateral view with the nasal bone near its resting orientation forming an angle of about 35° with the horizontal. B. The medial inclination of the upper margin of the corneo-scleral boundary in frontal view. C. The medial rotation of the nasal corneo-scleral margin seen in dorsal view. The upper extent of the rat binocular visual field as indicated by views of the two eyes at an elevation of D—30°, E—90°, F—50° from the rear, G—25° from the rear. The corneal vertex including the pupil is just visible from this position.

Table 3. Refractive state of rat schematic eyes

Lens model	K (diopters)	$H_{36}H'_{36}$	d (mm)	Axial length
Homogeneous	9.03	0.189	6.111	6.29
2-shell	4.616	0.030	6.111	6.29
2-shell emmetropic	0.000	0.030	6.178	6.357

tations would generate a population with a standard deviation of ± 1.7 D *arising from error of measurement alone.*

The averaging of from 6 to 14 measurements of parameters in Table 2 would reduce the significance of error of measurement and yet it is readily seen that the standard error of the mean of the average parameter values is very substantial relative to the estimated maximum errors of measurement, and indicates individual variation to be a more significant source of uncertainty. Compounding the standard errors of the mean parameter values throughout the computation of the core model schematic eye indicates the standard deviation of its refraction to be ± 5.7 D. However this result may be a gross overestimate of variation in the true population because pooling of the parameter values before calculation of refraction, rather than averaging of the individually computed refractions, eliminates the incorporation of any covariance between the parameters, e.g. a weak lens associated with a compensatingly stronger cornea.

The small variation in retinal thickness between animals indicates that the photoreceptor entrance aperture shell will have a standard deviation of its mean refraction of a similar magnitude to that of the more readily assessed vitread retinal surface. Retinoscopic refraction establishes the latter to have a mean refraction of 9.4 ± 1.8 D of hypermetropia. After Bessel correction the standard deviation of this refraction remains considerably smaller than the 5.7 D attributed to the schematic eye. If errors of measurement are indeed relatively unimportant as a source of variation then it might be concluded that there is significant covariance between the dimensions and powers of the rat eye components.

Systematic error. The mean refraction of the two shell schematic rat eye is ametropic. There are several possible sources of systematic error which would lead to apparent ametropia in even an emmetropic population.

Vakkur, Bishop and Kozak (1963) draw attention to the difficulty of ascertaining the *in vivo* thickness of the posterior wall of the globe because of possible emptying of the choroid of blood after death. The measurements on the rat eye employed swiftly ligated, enucleated and frozen eyes in which the choroidal blood may have been retained. Any emptying of the choroid would reduce the apparent hypermetropia; reduction of the hydrostatic pressure in the eye would increase it.

It has been pointed out that the choice of the lens model may considerably influence the mean refraction state of the schematic eye; the two shell model has been argued to be superior to the homogeneous model lens but its principal points may still not replicate those of the original eyes, so that there is the possibility of a systematic error arising out of the calculation itself. In addition there is the possibility that lens aberrations produce an increase in the back vertex distance over the true paraxial value because of the use of a finite 2 mm beam for its measurement. Both of these errors would tend to shift the mean refraction to hypermetropia.

Discussion

The mean refraction of the two shell schematic eye model is thus 4.6 ± 5.7 D (S.D.) of hypermetropia. It will be apparent that there is a 23% chance that this or a greater refractive error could be encountered after one such computation as detailed previously, even if the mean refraction obtained from many such computations indicated emmetropia. Quantitative assessment of systematic errors is thus hardly necessary.

It is worth noting that, although the mean refraction appears to be a substantial deviation from emmetropia, the actual separation of the effective image shell from the photoreceptor entrance apertures is very small. In order to convert the two shell schematic eye to an emmetropic condition it is only necessary to increase its axial length from 6.29 to 6.357 mm; this 0.067 mm adjustment amounts to only 1.1% of the length of the eye. A very small absolute error may thus suggest substantial ametropia in even emmetropic small eyes. Their refractive state is thus best assessed by means of differential optometric refraction. By this latter method the rat eye has been demonstrated to be nearly emmetropic when the pupil is small (Hughes, 1977a). That the ametropia of this schematic eye is not representative of the population of real eyes justified the inclusion of parameters for an emmetropic eye in Tables 2 and 3 for convenience when such a model is required.

ABERRATIONS

In an earlier publication (Hughes, 1977a) it was established that refraction of the retinal surface by means of a peripheral paraxial beam required some 6–8 D more power than with a central beam. In conjunction with the hypermetropia revealed by neurophysiological refraction when the pupil is large this was taken as evidence for the presence of overcorrected or negative spherical aberration.

The presence of positive or negative aberration may readily be discriminated in a ray diagram by noting whether the axial cusp formed by the verging rays points towards or away from the lens (Fig. 6a and b). The same effect may be observed when light is brought to a focus behind a lens immersed in fluorescein solution, as in Fig. 7a. The cusp which points towards the lens and the concentration of light in the rays *leaving* the focus proclaim the presence of

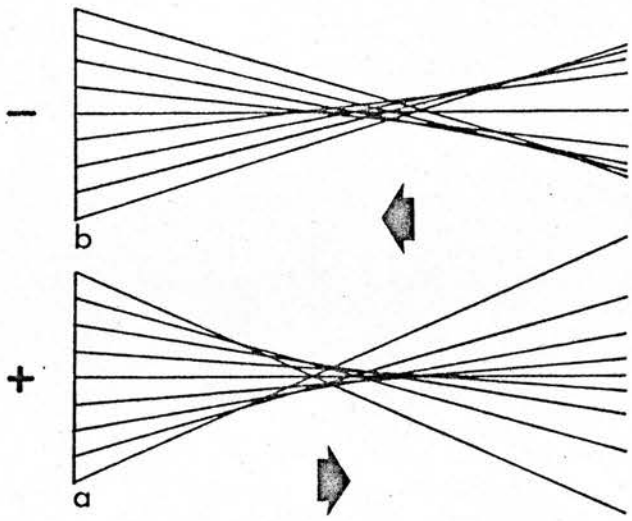

Fig. 6. Rays emerging from a lens showing the effect of positive aberration, *a*, and negative aberration, *b*. The axial cusp formed by the verging rays points away from the lens in the first situation and towards it in the second. The cusp may be made visible as a region of greater brightness when the rays pass through fluorescein solution.

strong negative aberration. Aberration of similar magnitude is visible in rays brought to a focus from a beam 30° oblique to the optic axis of the lens (Fig. 7b). A beam entering 75° oblique (Fig. 7c) appears to give rise to positive rather than negative aberration. It will be noted that the power of the lens for oblique rays appears to increase so that they are focused closer to the back vertex of the lens. Examination of the posterior retinal surface in cross sections of the rat eye shows that it approaches the lens in its more peripheral regions so that the increase in lens power seen in Fig. 7 will operate to ensure a satisfactorily focused retinal image.

The isolated lens of the cat also shows negative spherical aberration (Vakkur and Bishop, 1963) but the aberrations of the intact eye are not described. The majority of human eyes demonstrate under-corrected aberration of up to 3 D in the pupil margin when unaccommodated, but during accommodation it can change to an overcorrected aberration. The nature of the aberration differs from one meridian to another and is found in some subjects to be negative rather than positive. The much greater contribution of the rat lens to the overall power of the eye, 244 D:301 D, respectively, compared with the human eye, 20 D:60 D, may result in the negative abberation of the lens predominating over the positive aberration of the cornea to give an eye whose net peripheral aberration is opposite to that of the cornea dominated human eye.

POSTERIOR NODAL DISTANCE

The eye is an unequifocal system because the refractive index of the first and last media is different. The principal points thus no longer enjoy the property of being the axial points at which the object and image subtend equal angles. This property now belongs to the axial nodal points. Any paraxial ray incident on the first nodal point (N) will emerge from the system as though from the second nodal point (N') and will be parallel to the incident ray. The positions of the nodal points are given by:

$$PH = N'P' = +f = 3.326 \times 10^{-3}\,\text{m}$$

$$P'H' = NP = -f' = -4.446 \times 10^{-3}\,\text{m}.$$

The interval between the second focal point and the second nodal point, $N'P'$, is known as the posterior nodal distance.

The rat posterior nodal distance, *PND*, was obtained by the method of trans-scleral illumination in which the separation of the retinal images of two point sources set in front of the eye is measured, through the sclera, in photographs of the posterior wall of the eye or directly by means of a travelling microscope which is focused in the plane of the choroidal blood vessels. The *PND* is the product of the ratio of the image to the source separation with the source distance from the anterior nodal point of the eye. The average value for the *PND* determined in this fashion is given in Table 2 as:

$$PND = 3.39 \pm 0.03\,\text{mm (S.E.M. 6)}.$$

It is commonly suggested that the PND measured in this way overestimates the real value because the image is formed in layers of the globe posterior to the retina. In the pigmented rat this is unlikely to be a source of error because the image appears to be formed in the plane of the choroidal blood vessels and is thus only about 0.03 mm behind the photoreceptors. Vakkur, Bishop and Kozak (1963) employed their measurements of the *PND* of the cat eye in conjunction with its refractive state and vitreous humour refractive index as a basis for the computation of the posterior cardinal points. Obtained in this manner they provided a useful check upon the values arrived at quite independently by

computation of the schematic eye from the results of measurements on the dioptic apparatus of the real eye (Vakkur and Bishop, 1963). We may carry out a similar comparison for the rat eye.

Vakkur, Bishop and Kozak (1963, p. 303) develop the relationship which is required to establish the total power of an eye of refractive state, K, from its *PND*. If we assume the rat eye to be emmetropic when the pupil is small in accordance with the results of the preceding paper (Hughes, 1977a) then the situation is simplified and the required total power is simply the reciprocal of the PND for the eye in air. From the mean *PND* of Table 2 we thus have:

$$F = 295.0 \pm 2.6\,\text{D (S.E.M. 6)}$$

and the posterior principal point is situated:

$$1.337/295.0 = 4.532 \pm 0.04\,\text{mm (S.E.M. 6)}$$

in front of the posterior focal point. Both results are within 2% of those obtained during the computation of the rat schematic eye (Table 2); the independence of the results obtained by the two methods is again emphasised.

The *PND* might be expected to be of equal magnitude to the radius of curvature of the photoreceptor plane as was described for the cat (Vakkur and Bishop, 1963) and rabbit (Hughes, 1972). From Table 2 the curvature of the posterior scleral wall is seen to be given as:

$$3.23 \pm 0.022\,\text{mm (S.E.M. 10)}$$

from measurements on sections of the frozen globe. The radius of curvature of the photoreceptor plane is 0.14 mm less than this at 3.09 mm which is about 90% of the measured *PND*. A similar discrepancy occurs in the human eye in which the schematic *PND* value of 17.0 mm is matched by a radius of curvature at the photoreceptor plane of only 12.0 mm; with a ratio of 0.7 this is a much poorer fit than that of the rat. The explanation of the discrepancy in the human eye (Bennett and Francis, 1962) is that the perfect correspondence of the radius of curvature and the *PND* is only advantageous if oblique astigmatism is compensated for and the images are formed on the Petzval surface. The real retina occupies a position bridging the tangential and sagittal image shells to which the images are brought by the undercorrected oblique astigmatism. It is possible that a similar explanation applies to the rat eye but why it should differ from those of the cat and rabbit is difficult to conceive; the discrepancy, however, is only small.

The observed *PND* of 3.39 mm means that, in the emmetropic eye, one degree in the visual field near to the optic axis is represented by

$$\frac{2\pi\,3.39}{360} = 0.0592\,\text{mm/deg}$$

along the retina in the photoreceptor plane. The schematic eye suggests the corresponding value of 0.057 mm/deg.

A few more measurements of the *PND* were made on rapidly enucleated and ligatured eyes in order to establish its value at points well away from the optic axis. The results for the on axis measurements were similar to those of the *in vivo* set; no difference could be detected between on axis determinations and those made 50° nasal or temporal.

Given the mean uniocular field of 200° for the rat eye (see below) and assuming that the *PND* remains constant out to the ora serrata, we would expect the retina to be $200° \times 0.059 = 11.8$ mm long, whereas carefully extracted retinas which are apparently intact to the ora serrata never exceed 10 mm and are usually about 9.5 mm in breadth. It must therefore be concluded that the *PND* is reduced towards the periphery.

If the theoretically determined posterior nodal point is appropriately marked on the section through the frozen rat eye of Fig. 6 then it is found that the retinal boundaries determined by the ora serrata subtend an angle of 180° at its position; within this sector must be represented 200° of the external visual field. Of this, 100° are established as enjoying a magnification equal to that on the axis and occupying $100° \times 0.0592 = 5.92$ mm. The remaining 100° of visual field must be squeezed into an internal sector of 80° and thus occupy $80°/100° \times 5.92 = 4.74$ mm of retina. On this basis the retina is $4.74 + 4.92 = 10.66$ mm long. Measurement of the distance from the photoreceptor plane to the posterior nodal point in the periphery of the eye indicates a reduction to about 85% of the axial value in support of the above suggestion, but the retina of Fig. 6 is measured to be only 10.19 mm in length so the reduction in peripheral *PND* must actually be somewhat greater than is suggested above. The somewhat greater mean length of retinas measured in sections of the frozen globe (+0.5 mm) when compared with the extracted but unfixed and flattened organ may indicate that it is under slight tension when *in situ*.

ENTRANCE AND EXIT PUPILS OF THE AVERAGE SCHEMATIC EYE

Entrance pupil

Light entering the eye is limited in object space by the margins of the entrance pupil, the image of the real pupil formed by the cornea. Similarly, the exit pupil or image of the real pupil in the crystalline lens determines the extent of the ray bundle which forms the image of a point source. The relative sizes and positions of the entrance and exit pupils varies with the position and size of the real pupil and must be computed for the circumstances of interest.

The pupil margin is defined by the plane of contact of the iris with the anterior surface of the crystalline lens and it thus retreats from the cornea as the pupil opens. The apparent position of the pupil, that is, the distance of the entrance pupil from the cornea, l, is given by the inverse of the vergence of the rays from the pupil margin when emergent from the cornea:

$$l = \left(\frac{n_3}{l'} - F_{12}\right)^{-1} \qquad (4)$$

Bennet and Francis (1962). The geometry of the lens enables the distance of the real pupil from the cornea,

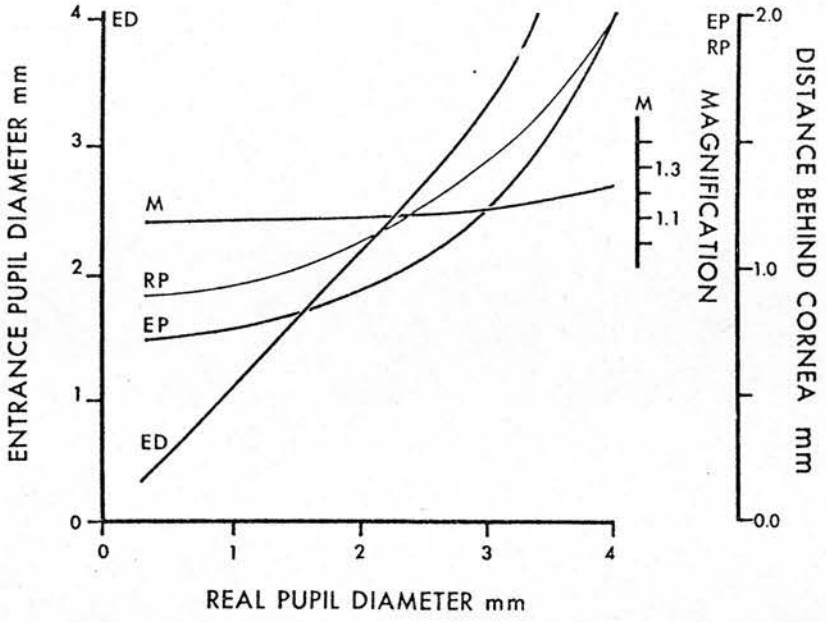

Fig. 8. Entrance pupil diameter, *ED*, magnification relative to the real pupil, *M*, and distance behind the cornea, *EP*, plotted against the real pupil diameter. The real pupil position, *RP*, is included for comparison with that of the entrance pupil. The curves are computed according to the method of Bennett and Francis (1962). The entrance pupil always remains somewhat forward of the real pupil.

l, to be computed. The magnification, m, of the entrance relative to the real pupil is given by

$$m = \left(\frac{n_3}{l'}\right) \Big/ \left(\frac{n_3}{l'} - F_{12}\right). \qquad (5)$$

The results of computations of entrance pupil position, size and magnification for various real pupil diameters are plotted in Fig. 8.

Exit pupil

The exit pupil is an image of the real pupil formed by the crystalline lens itself; the simplified homogeneous or core model lenses used in schematic eye computation are thus inevitably limited in their usefulness for predicting its dimensions and position. The model lenses were developed for paraxial rays limited to bundles close to the optic axis; their inadequacy for quantitative prediction of spherical aberration has been mentioned already. Given that for most purposes involving computation of the exit pupil a high degree of accuracy is not required, *we may accept the limitations of the homogeneous rather than core lens and gain some simplification of computation.* The method of vergence computation employed for the entrance pupil is applicable in the case of the exit pupil computations but does not take into account the off axis aberrations. Again, the positions of the lens principal planes and its focal lengths may be employed to compute the exit pupil but in the homogeneous lens the principal planes actually approach each other away from the axis so that for large pupils this method can give considerable error. Such computation places the exit pupil 0.483 mm behind the 10.0 mm diameter cat real pupil (Vakkur and Bishop, 1963) whereas a ray trace indicates its position to be 0.903 mm behind.

The exit pupil position may thus be obtained by any of the standard methods if the real pupil is small, although a ray trace must be computed rather than worked geometrically. The position of larger exit pupils may now be determined only by computed or geometrical ray traces once the inevitable limitations of the available lens models have been accepted.

The standard dimensions of the average eye enable the angle of incidence, i and i', of two selected and well spaced rays from the real pupil to be calculated by trigonometry. Snell's law then determines the angles of refraction from which α, β and d may be determined (Fig. 9). Substituting in

$$h = \frac{d}{\cot\beta - \cot\alpha} \qquad (6)$$

we find h, the radius of the exit pupil, from which it is straightforward to compute the position.

The ray traces for several sizes of real pupil have been calculated and the resulting plot of exit pupil position, size and magnification is shown in Fig. 10. The results of computing these parameters of the exit pupil by the vergence method of Bennet and Francis (1962) are also displayed for comparison. Unlike the case of the cat, the discrepancy between the computations is not large so that, unless great accuracy is required, the vergence method may be regarded as pragmatically justified for the rat, and is much quicker to use.

It will be noted that, for almost the whole range of pupil sizes in the rat, the exit pupil is cornead of the entrance pupil which is itself cornead of the real pupil. In comparison with the cat, the exit pupil is shifted forward a considerable distance.

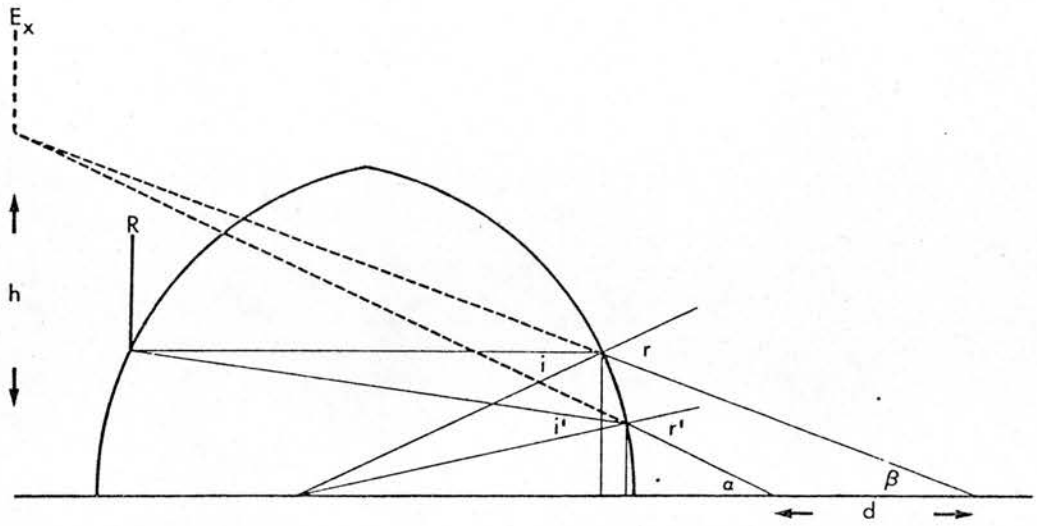

Fig. 9. Construction for the determination of the exit pupil position, diameter and magnification relative to the real pupil by means of a computed ray trace. Details in text.

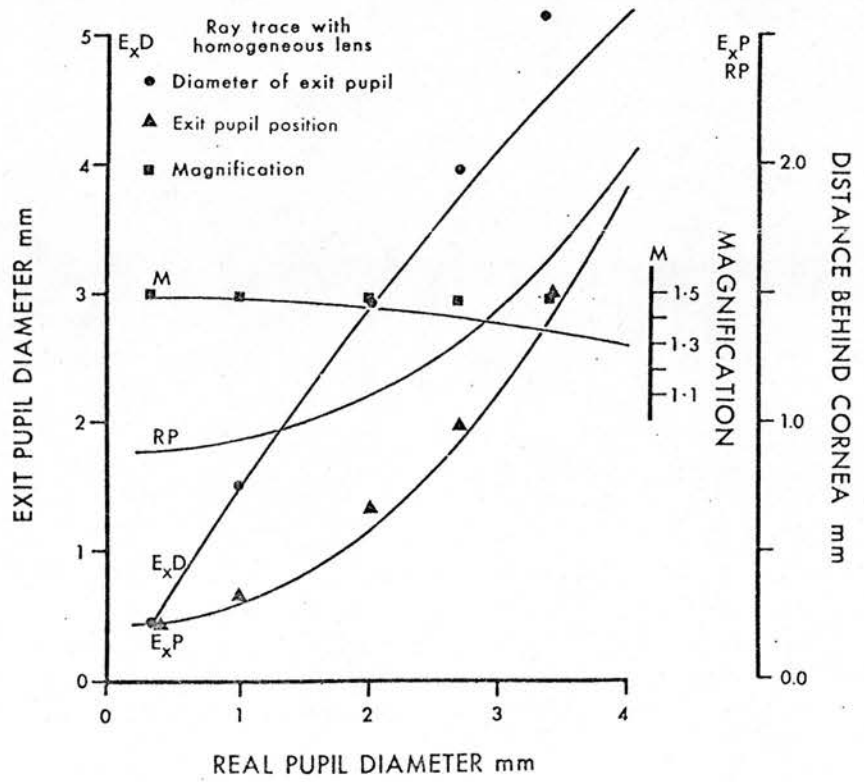

Fig. 10. Exit pupil diameter, E_xD, magnification relative to the real pupil, M, and distance behind the cornea, E_xP, plotted against the real pupil diameter. The real pupil position, RP, is included for comparison with that of the rat, the exit pupil is also invariably situated in front of the entrance pupil. The curves are computed according to the schedule of Bennett and Francis (1962). The diameter, position and magnification of the exit pupil as determined by computed ray traces according to the method outlined in the text and Fig. 9 are also plotted as points, according to the convention outlined in the illustration, which represents the results of individual computations.

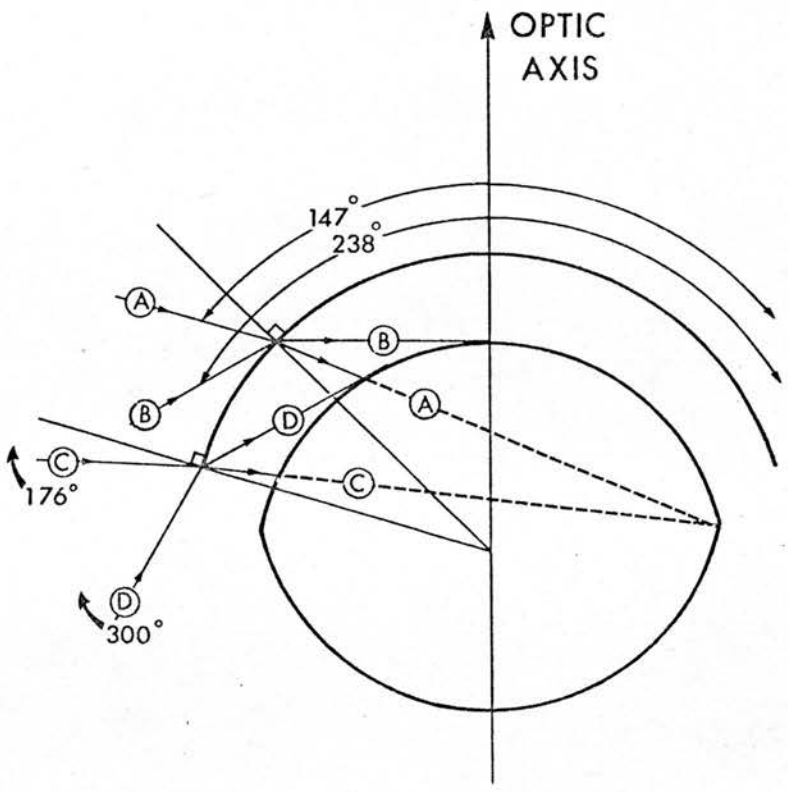

Fig. 11. The limits of the rat uniocular field as estimated from the results of the schematic eye. The limiting ray lies between rays A and B when the pupil is small. When the pupil is large, unlike the cat where the lens is not set so far forward relative to the cornea-scleral boundary, a different set of limiting rays apply—C and D. No ray as eccentric as D could in reality reach the retina even if it was refracted into the lens.

SCHEMATIC VISUAL FIELD

Theoretical monocular field of view

It is possible to use the schematic eye to calculate the limits of the monocular field of an enucleated eye (Vakkur and Bishop, 1963). Any light ray incident upon the lens whose extension intersects its equatorial margin will be refracted into the vitreous humour. Thus, in Fig. 11, the ray A is directed towards the lens equator and has an angle of refraction of 21° at the cornea. Assuming that the cornea is a single refracting surface of refractive index 1.38, we find the angle of incidence of this ray to be 29.6°. If the eye is symmetrical about the optic axes this leads to a minimum visual field of 147°. The upper limit on the extent of the visual field (when the pupil is small) is determined by ray B which grazes the lens tangentially and is not refracted. This ray must have an angle of incidence of 84° so that the total visual field is less than 238° in extent. Its actual value depends upon the optics of the peripheral lens which cannot be dealt with sufficiently accurately to make further computation profitable. The mean of the above limiting values is 192.5°, which is quite close to the observed extent of the rat monocular field.

The larger pupil enables the entry into the lens of more eccentric rays from the cornea periphery. The theoretical lower limit of the uniocular field has increased to 176° with ray C, but the upper limit with a large pupil of 300°, indicated by ray D, has not been approached in the real eye.

Monocular field of the enucleated eye

The monocular field of view of the enucleated eye, free of obstruction by the eyelids or body, was determined from measurements of the ophthalmoscopically observed limits of the retinal light reflex when the eye was centred in a perimeter. Only rapidly enucleated and ligatured eyes were used; the eye was not pressurised from a hydrostatic reservoir as there is a risk of disturbing the optical system upon the insertion of the necessary needle. The monocular field of the isolated eye was found to extend for 205° along the horizontal (mean of 4); a portion of the nictitating membrane was retained for the orientation of the eye. The field appeared to be equally extensive in the vertical plane.

The field of view was also determined by the transcleral viewing of the image of a light moved around the perimeter arm. By this means the extent of the horizontal visual field was found to be only 195°.

The mean of the two sets of results for the monocular fields of view was thus 200°, which lies comfortably between the limits set by the theoretical considerations presented earlier.

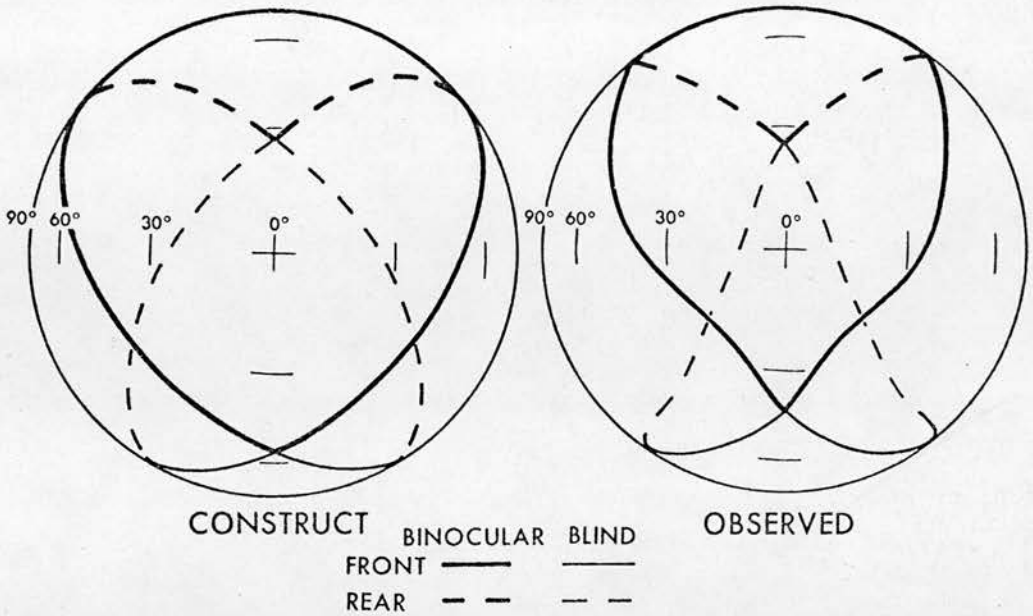

Fig. 12. The theoretically constructed potential binocular field of the rat as projected onto the surface of a sphere distant from the animal's head. The viewpoint lies on an axis passing from the centre of the sphere through the point of intersection of the midsagittal plane with the nasal region of the equator. The *observed* binocular and monocular front and rear limits of the visual field of an anaesthetised rat are also plotted according to the same convention for comparison. The results are similar to the theoretical predictions except in that the actual binocular field is some 20° narrower on the equator.

Theoretical binocular field

The projection of the optic nerve head relative to the horizontal and midsagittal planes was determined for six anaesthetised and six dead rats; no significant difference was found between them and examination of tranquilised rats with a hand held ophthalmoscope indicates that the optic nerve head occupies a similar position in the fairly conscious animal. The optic nerve head was found to have a mean projection of 58° temporal of the anterior vertical meridian (0°) and to be elevated 30° above the horizontal plane.

Examination of preparations of eight flat mounted retinas revealed the optic nerve head to be situated centrally in the retina; the ophthalmoscopically determined limits of the monocular field of the eye were found to be symmetrical with respect to the optic nerve head projection, which confirms this observation.

Given the projection of the optic nerve head, its central position and a monocular field extending some 200°, it is possible to employ nomographic methods to determine the theoretical monocular and binocular whole field free from obstruction by head and body. The results of such a computation are shown in Fig. 12 where the binocular field and corresponding blind area are projected onto a sphere centred on the animal's head and large enough to make the interocular distance negligible. The viewpoint lies on an axis passing from the centre of the sphere through the point of intersection of the midsagittal plane with the nasal region of the equator. The region of overlap between the left and right monocular fields defines the unobscured binocular field.

The binocular field of the rat is thus seen to be extensive in *theoretical* construction; on the equator it is some 100° wide.

Visual field in vivo

The ophthalmoscopically observed limits of the retinal light reflex were used to determine the total extent of the monocular and binocular fields of view of three *intact* anaesthetised rats. The results were similar and are shown for one characteristic animal in Fig. 12. The head of the animal was horizontal so that the nasal bone formed an angle of 35° to the horizontal (Fig. 13).

The actual binocular field begins some 40° below the horizontal where the nose obscures the potential field and extends to 65° beyond the vertical at the rear. The medial intrusion of the monocular field into the opposite half field is greatest in the superior nasal quadrant and amounts to just over 40°. The maximum width of the binocular field is thus about 85° compared with the theoretical 100°. The overall form of the theoretical and real binocular fields is very similar, as may be seen in Fig. 12 where the observed results are portrayed in a similar fashion to the theoretical for comparison. The large extent of the rat binocular field *in vivo* may be seen in photographs of the head, e.g. Fig. 13a, b, c.

The projection of the optic nerve head and the magnitude of the binocular field as computed and demonstrated in the previous sections depend upon observation of the dead, anaesthetised or tranquilised rat, and if suggested as representing the situation in the normal animal may justifiably be regarded with suspicion. Some results of Montero, Brugge and Beitel (1968) may, however, support such a claim.

Montero *et al.* (1968) mapped the ipsi- and contralateral inputs to the L.G.N. of one rat whose optic nerve heads projected to coordinates of +25° and 75° temporal in the visual field. One unit was recorded whose receptive field could be mapped through both ipsi- and contralateral eyes. The coordinates of the ipsilateral receptive field were +25° and 10° T. and those of the contralateral receptive field were +20° and 50° T. It is probable that these fields are located in conjugate regions of the two retinas so that the eye positions required for their fusion are the same as when viewing distant objects; such fusion may be achieved by a 20° nasal rotation of each eye in the horizontal plane which brings the optic nerve head projections to 75° − 20° = 55° temporal; within 3° of the 58° temporal specified earlier and supporting the representation of this as the physiological resting position.

The 140° binocular field of cat and man (Vakkur and Bishop, 1963) is only 1.6 times wider than that of the rat—85°—whereas it is 6.0 times wider than the 24° binocular field of the rabbit. By contrast, the 200° whole field of cat and man is much smaller than that of either the rat—320°—or rabbit—360° (Hughes, 1971).

The possession of an extensive visual field by the rat may be accounted for by its similarity to the rabbit, and difference from man and cat, in being subjected to predation both when young and, less extensively, when full grown. Dogs, cats and other species may take rats; they were found in the stomachs of some 13% of foxes examined after myxomatosis had limited the availability of rabbits (Lever, Armour and Thompson, 1957).

The prime advantage of a binocular field of view may be accepted as its potentiality for providing stereopsis. Examination of the projection of the ipsilateral visual field onto the rat primary visual cortex (Adams and Forrester, 1968) reveals a representation of the binocular field which is 50° across at the level of the optic nerve head projection—a total binocular representation of 100° as theoretically computed earlier. Similar representations of the small rabbit binocular field (Thompson, Woolsey and Talbot, 1950; Hughes, 1971) and cat binocular field (Hubel and Wiesel, 1962) are also found. In cat and man the ipsilateral input to the cortex is regarded as providing for stereopsis; there is no obvious reason for withholding this explanation from the rat and rabbit.

Whatever the multifactorial explanation for the development of panoramic stereopsis (Hughes, 1977b), there would be some evolutionary trading off of its advantages against the need to sequentially scan the blind region induced to the rear of the head. A correlation might thus be expected between the extent of panoramic stereopsis attained by a given species and the importance of stereopsis in its life style. This qualitatively exists for the series cat, rat and rabbit. The rat, with its intermediate extent of binocular field, is not so dependent upon distance judgement and manipulation as cat and man but it nevertheless employs these skills to a much greater degree than the rabbit; even the brown rat is a superlative climber relative to the rabbit. Panoramic stereopsis would again be of undoubted value in hunting and, whereas the rabbit is never predatory in its behaviour, the rat may readily take to carnivorous habits and eat not only insects but also mice whose everted skins may be found in quantity near some rat colonies (Southern, 1964).

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A SCHEMATIC EYE FOR THE RABBIT

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(*Received* 18 *August* 1971)

INTRODUCTION

THE AUTHORS of a recent exhaustive study of the cat eye have commented on the shortage of optical information relating to the animal eye (VAKKUR, BISHOP and KOZAK, 1963). The optics of the rat eye have been treated by LASHLEY (1932) and a schematic eye for that animal has been presented by both HERMAN (1958) and BLOCK (1969).

The anatomy of the rabbit eye has been qualitatively examined in some detail (DAVIS, 1929; SHEPPARD, 1961) and several papers are available that present quantitative information about the components of the rabbit optical system but it has not yet been brought together for the calculation of a schematic eye. A recent volume devoted to the rabbit eye does not contain a discussion of its optics (PRINCE, 1964). A schematic eye has consequently been developed on the basis of the computing schedule described by D. A. Gullestrand in the English translation of HELMHOLTZ's *Handbuch der Physiologischen Optik* (1909–1911). The calculation has, however, been simplified by the assumption of a homogeneous lens.

The power of the rabbit cornea and lens undergoes considerable change in the first 30 weeks of life. These changes are probably the necessary concomitant of the increase in size of the eye during growth. The mediolateral dimension of the newborn rabbit eye is about 6 mm; the adult value is in the order of 18·0 mm. The human eye undergoes an axial elongation of only 6·0 mm in post-natal growth. In selecting optical data from the literature it is consequently necessary to ensure that young rabbits were not used as experimental material. The information presented in the following pages was obtained by observations made on the eyes of animals weighing between 2·0 and 3·0 kg—the same range of size as used in the experimental work for which the study formed the background.

Calculation of the schematic eye begins with the use of thick lens theory to develop an equivalent thin lens for the cornea and for the crystalline lens. The calculation is completed when a further thin lens is derived to represent the behaviour of the whole eye by the combination of the equivalent thin corneal and crystalline lenses. The model is valid for the axial rays alone. The experimental methods have been included in the data section which precedes each step in the calculation.

CALCULATION

The cornea

Data

Cornea refractive index. VAKKUR and BISHOP (1963) assume the refractive index of the cat cornea to be the same as the value accepted for man (1·376 in Gullstrand's schematic eye). An Abbé refractometer was used to determine the refractive index of the rabbit cornea immediately after its removal from an anaesthetised animal. The measurements were

carried out at room temperature. The average of measurements made on three animals was 1·376 to three significant figures. The value may be justified for application to the intact living eye by back calculation from the measured total corneal power and the known corneal radii of curvature.

Aqueous humour refractive index. VALENTIN (1879) reports a value of 1·337 as the refractive index of the rabbit aqueous humour. FREYTAG (1910) obtained a range of values from 1·33 to 1·329 for animals of between 9 days and 5 years of age. Samples of fresh aqueous humour withdrawn from the anterior chamber by hypodermic syringe gave an average value of 1·337. This latter value will be used in the ensuing calculations.

Curvature of cornea. The radius of curvature of the anterior corneal surface has been measured by several workers; PRINCE (1964) quotes 7·0–7·5 mm; DAVIS (1929), 7·3 mm; SORSBY and SHERIDAN (1953), 7·5–8·25 mm. Keratometer measurements carried out by the author gave readings from 7·3 to 7·8 mm on adult rabbits. For the following calculations the anterior corneal radius of curvature has been assumed to be 7·5 mm.

The inner corneal surface has been assumed to be concentric with the anterior surface. Its radius of curvature is less than that of the anterior surface by the apical corneal thickness. The reader is referred to PRINCE (1964) for a discussion of corneal thickness—a value of 0·4 mm is assumed here.

Conventions. The following conventions are observed in the ensuing calculations. Light rays enter the system from left to right; the refractive indices of the media encountered are numbered in the same direction beginning with air, n_1; surfaces are numbered in the order encountered, beginning with the anterior vertex of the cornea, A_1, which is used as a reference point for the measurement of distances. Measurements to the right of A_1 are positive. Surfaces convex to the light are defined as having positive radii of curvature (r). The first principal point of a system is indicated by a suffixed capital letter, e.g. H_{12}; the second principal point is represented similarly but bears an apostrophe.

Calculation

The refracting power of the anterior surface of the cornea is

$$F_1 = \frac{n_2 - n_1}{r_1} = \frac{(1{\cdot}376 - 1) \times 10^3}{7{\cdot}5} = +\,50\text{D} \tag{1}$$

and that of the posterior surface is

$$F_2 = \frac{n_3 - n_2}{r_2} = \frac{(1{\cdot}337 - 1{\cdot}376) \times 10^3}{7{\cdot}1} = -\,5{\cdot}5\text{D}. \tag{2}$$

The reduced interval (GULLSTRAND, 1924) between the two surfaces is

$$C_1 = \frac{A_1 . A_2}{n_2} = \frac{4{\cdot}0 \times 10^4}{1{\cdot}376} = 2{\cdot}9 \times 10^{-4}\text{m}. \tag{3}$$

If F_{12} denotes the refracting power of the corneal system where

$$F_{12} = F_1 + F_2 - C_1 . F_1 - F_{12} \tag{4}$$

then

$$F_{12} = 50 - 5{\cdot}5 - 2{\cdot}9 . 10^{-4} . 50 . (-5{\cdot}5) = 44{\cdot}6\text{D}. \tag{5}$$

The principal points of the cornea system are given by

$$A_1H_{12} = \frac{C_1.F_2}{F_{12}} = \frac{2{\cdot}9.10^{-4}\,(-\,5{\cdot}5)}{44{\cdot}6} = -\,0{\cdot}36 \times 10^{-4}\text{m}. \qquad (6)$$

We assume H_{12} to be equal to A_1.

$$A_2H_{12} = \frac{C_1F_1n_3}{F_{12}} = \frac{-\,2{\cdot}9.10^{-4}.1{\cdot}337.50}{44{\cdot}6} = -\,4{\cdot}35 \times 10^{-4}\text{m} \qquad (7)$$

and thus $A_1H'_{12} = -0{\cdot}4$ mm.

The schematic corneal power of 44·6D is in quite good agreement with published values for the adult rabbit. STONE and LEARY (1953) report that the corneal power stabilizes at 42D in the 60th post-natal week. CHOU (1954) reports a final value of 45D attained after 40 weeks while SORSBY, BENJAMIN, SHERIDAN, DAVY and TENNER (1957) find 43D to be average value for adult British rabbits.

The crystalline lens

Data

Position. The crystalline lens lies 2·9 mm behind the posterior corneal surface. This distance is achieved in the 20th post-natal week and afterwards remains constant (Sorsby, STONE, LEARY and SHERIDAN, 1960).

Anterior curvature. The anterior radius of curvature of the lens reaches a value of 7·0 mm in the 60th post-natal week and remains constant afterwards (SORSBY *et al.*, 1960). Keratometer measurements on the excised lenses of rabbits weighing more than 2·5 kg are less satisfactory than those which Sorsby *et al.* obtained from the intact eye by photographic ophthalmophakometry but are essentially in agreement. Measurements on twelve rabbits averaged 6·9 mm. The value of 5·0 mm suggested by PRINCE (1964) is very low.

Thickness. The lens of the rabbit is rather thick; PRINCE (1964) reports a value of 7·0 mm. SORSBY *et al.* (1961) do not give details but estimate a range from 8·0 to 10·0 mm. Measurements in this series were made on enlargements of photographic dorsal views of twelve isolated lenses standing vertically, supported by a small cup, in a bath of isotonic saline. A range from 7·0 to 8·6 mm was obtained with the average of twelve measurements as 7·9 mm.

Radius of curvature. The radius of curvature of the rear surface of the lens is not readily obtained from the intact eye because of the thickness of the lens. Prince suggests a value of 5·0 mm. Measurements made on photographs of 12 excised lenses gave an average value of 5·8 mm.

Refractive index. The crystalline lens consists of a capsule that contains a core of rather higher refractive index. VALENTIN (1879) gives the value of 1·448 for the lens core; Freytag described a range from 1·417 to 1·465 for animals from nine days to 5·5 years of age (1910). Freytag found the index to vary more in rabbits between the young and the old individual than in any other animal he investigated.

The Abbé refractometer has been used to measure the refractive index of both capsule and core in the present investigations. The capsule, when blotted dry, gave readings ranging from 1·407 to 1·412. The core gave readings from 1·43 to 1·46. These readings are included for the sake of completeness rather than for use in the schematic eye calculations. The gradient of refractive index through the lens makes it impossible to develop a schematic eye

with the simple lens formulae. The effect of the core is to increase the power of the lens relative to a homogeneous lens of the same refractive index as the core. It is thus possible to represent the lens by an equivalent organ of identical shape but of uniform and higher refractive index. The refractive index of the equivalent, homogeneous, lens is known as the total or overall refractive index of the lens. The literature appears to contain no measurements of the total refractive index of the rabbit lens. SORSBY *et al.* (1961) give reasons to support the view that it is about 1·6. An estimate of its value was obtained in the following fashion.

The distance from the posterior vertex of the lens to the posterior focal point was measured. A source of nearly parallel light was placed at a distance of 2 m in front of the excised lens; the image of the source was focused on a screen affixed to the end of a micrometer screw placed behind the lens. The micrometer reading was taken at the position of best focus and at the posterior vertex of the lens. The inverse of the difference between these two readings may be taken, without much error, to be the back vertex power of the lens in air (expressed in diopters when the distance is measured in meters). An average reading for 12 lenses was 3·8 mm to one decimal place. The back vertex power in air is thus 263D.

In order to test the suggested value of 1·6 for the effective lens refractive index we now assume the figure and use thick lens theory to calculate the back vertex power in air. A good agreement between the theoretical and experimentally determined values will justify the assumed refractive index.

Using parameters averaged from 12 lenses we have for the anterior surface power of the lens in air,

$$F_{3a} = \frac{(n_4 - n_1) \times 10^3}{r^3} = \frac{(1{\cdot}6 - 1) \times 10^3}{6{\cdot}9} = 87\text{D}. \tag{8}$$

The posterior surface power is given by

$$F_{4a} = \frac{n_1 - n_4 \times 10^{-3}}{r_4} = \frac{(1 - 1{\cdot}6) \times 10^3}{-5{\cdot}8} = 103\text{D}. \tag{9}$$

Thick lens theory gives the refracting power of the lens in air to be

$$F_a = F_{3a} + F_{4a} - t.F_{3a}.F_{4a} = 103 + 87 - 4{\cdot}9 \times 10^3.87.103 = 146\text{D}. \tag{10}$$

The posterior vertex power Vpa in air is then given by

$$Vpa = \frac{F_a}{\left(1 - \frac{t}{n_4} F_{3a}\right)} = \frac{146}{1 - \frac{7{\cdot}9 \times 10^{-3}}{1{\cdot}6} \cdot 87} = \underline{256\text{D}}. \tag{11}$$

The average of six observations of the posterior vertex power in air gave 263D. The agreement between the theoretically determined value of 256D and the measured 263D is close enough to justify the use of the value 1·6 for the total refractive index of the lens.

Calculation

We may now calculate the equivalent thin lens for the crystalline lens immersed in aqueous and vitreous humours. For the anterior surface power we have:

$$F_3 = \frac{(n_4 - n_3) \times 10^3}{r_3} = \frac{(1{\cdot}6 - 1{\cdot}337) \times 10^3}{6{\cdot}9} = 38\text{D}. \tag{12}$$

For the posterior surface power

$$F_4 = \frac{(n_5 - n_4) \times 10^3}{r_4} = \frac{(1{\cdot}337 - 1{\cdot}6) \times 10^3}{-5{\cdot}8} = 45\text{D}. \tag{13}$$

If the refracting power of the lens system as a whole is denoted by L then,

$$L = F_3 + F_4 - s.F_3.F_4 \tag{14}$$

where the reduced thickness is denoted by s

$$s = \frac{7{\cdot}9 \times 10^{-3}}{1{\cdot}6} = 4{\cdot}9 \times 10^{-3}\text{m} \tag{15}$$

we find that

$$L = 38 + 45 - 4{\cdot}9 \times 10^{-3}.38.45 = 75\text{D}. \tag{16}$$

The back focus distance, d_b, of the lens in saline—or aqueous and vitreous humours—is given by

$$d_b = \frac{1{\cdot}337\,(1 - s.F_3)}{L} = \frac{1{\cdot}337\,(1 - 4{\cdot}9 \times 10^{-3}.38)}{75} = 14{\cdot}5 \text{ mm}. \tag{17}$$

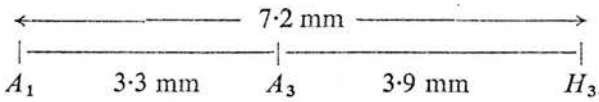
As a second confirmation of the assumed total refractive index, d_b was measured for six lenses. The lenses were placed in a saline bath containing fluorescein on the axis of a light beam convergent 30 m further on. A vernier microscope suspended over the bath with its track parallel to the light beam was used to measure the distance from the rear vertex of the lens to the plane of least confusion of the light rays leaving the lens. The average distance for six lenses was 15·0 mm which is in quite good agreement with the predicted value of 14·5 mm. The primary principal point of the lens system, H_{34}, is given by

$$\frac{A_3H_{34}}{n_3} = \frac{s.F_4}{L} \therefore A_3H_{34} = \frac{4{\cdot}9 \times 10^{-3}.45.1{\cdot}337}{75} = 3{\cdot}9 \times 10^{-3}\text{m}. \tag{18}$$

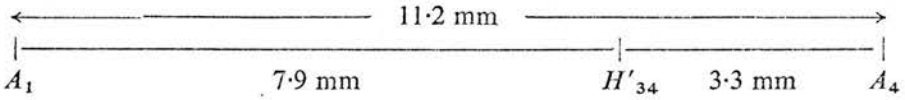
The second principal point, H'_{34}, is given by

$$\frac{A_4H'_{34}}{n_3} = \frac{-s.F_3}{L} \therefore A_4H'_{34} = \frac{-4{\cdot}9 \times 10^{-3}.38.1{\cdot}337}{75} = -3{\cdot}3 \times 10^{-3}\text{m}. \tag{19}$$

The first principal point of the lens lies in the following relationship to the anterior corneal vertex.



So that A_1H_{34} is 7·2 mm. The second principal point lies in relationship to A_1 as follows.



So that $A_1H'_{34}$ is 7·9 mm.

The schematic eye

Calculation

We are now in a position to combine the cornea and lens systems to obtain the parameters of the schematic eye. The refracting power of the optical system of the whole eye is given by

$$F = F_{12} + L - C.F_{12}.L \tag{20}$$

where the reduced distance C is the distance between the second principal point of the corneal system and the first principal point of the lens system divided by the refractive index of the aqueous humour. H'_{12} is at A_1 so

$$C = \frac{H'_{12}H_{34}}{n_3} = \frac{7{\cdot}6 \times 10^{-3}}{1{\cdot}337} = 5{\cdot}7 \times 10^{-3}\text{m} \tag{21}$$

and $F = 44{\cdot}6 + 75 - 5{\cdot}7 \times 10^{-3}.44{\cdot}6.75 = 100{\cdot}6\text{D}.$ (22)

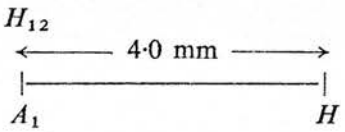
The first principal point of the schematic eye is given by

$$H_{12}H = \frac{CLn_1}{F} = \frac{5{\cdot}4.10^{-3}.75{\cdot}1}{100{\cdot}6} = 4{\cdot}00 \times 10^{-3}\text{m}. \tag{23}$$

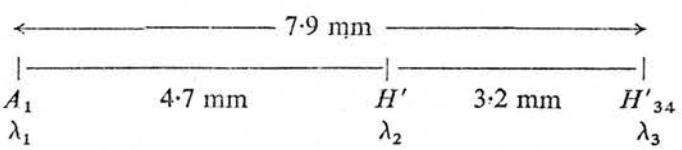
The second principal point is given by

$$H'_{34}H' = \frac{-C.F_{12}n_5}{F} = -\frac{5{\cdot}4.10^{-3}.44{\cdot}6.1{\cdot}337}{100{\cdot}6} = -3{\cdot}2 \times 10^{-3}\text{m}. \tag{24}$$

The first principal point lies in the following relationship to A_1.



So that A_1H is 4·0 mm.
The second principal point lies in relationship to A_1 as follows.



So that A_1H' is 4·7 mm.

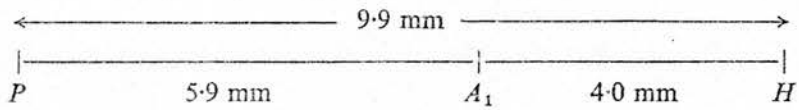
If the focal lengths of the eye are denoted by f and f' we have

$$f = \frac{n_1}{F} = \frac{1}{100{\cdot}6} = 9{\cdot}9 \text{ mm} \tag{25}$$

$$f' = -\frac{n_5}{F} = -\frac{1{\cdot}337}{100{\cdot}6} = -13{\cdot}3 \text{ mm}. \tag{26}$$

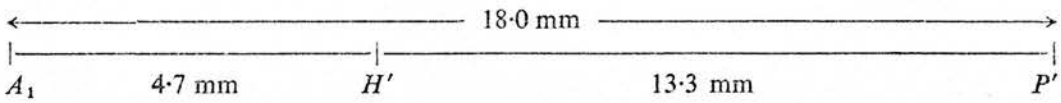
The focal point P and P' are thus located as follows

$$A_1H - f = A_1P = 4{\cdot}0 - 9{\cdot}9 = -5{\cdot}9 \text{ mm} \tag{27}$$



and

$$A_1H' - f' = A_1P' = 4{\cdot}7 - (-13{\cdot}3) = 18{\cdot}0 \text{ mm} \tag{28}$$



The refractive state of the rabbit eye

The refractive condition of the rabbit schematic eye cannot be determined without an estimate of the distance along the optic axis from the anterior corneal vertex to the photoreceptor layer.

Data

Mediolateral dimension. ROCHON-DUVIGNEAUD (1943) has given a mediolateral measurement for the globe of 17–18 mm. LAND (1957) finds the average mediolateral dimension for ten rabbits weighing more than 2·5 kg to be 18·5 mm in the American animal which is larger than the European. SORSBY *et al.* (1960) find the adult mediolateral dimension for British rabbits to be 18·0 mm.

The mediolateral dimension of the globe, cleared of muscle attachments, was determined by micrometer for six eyes inflated to an internal pressure of 30·0 cm of water by means of a hypodermic needle connected to an adjustable saline reservoir inserted into the vitreous humour. The average of the measurements was 18·1 mm and this is the figure assumed in the subsequent calculations.

Thickness of sclera and choroid. In the emmetropic state the image should be brought to a focus in the plane of the photoreceptor layer which is some distance in front of the posterior scleral surface. The scleral thickness varies considerably but under the visual streak it is less than 0·2 mm thick (PRINCE, 1964). In the same area the choroid is about 0·036 mm thick (PEREGRINE and DODT, 1969). The overall distance from the posterior scleral surface and the photoreceptor layer may thus be taken as about 0·2 mm.

Calculation

Schematic eye refractive error. The distance from the anterior corneal vertex to the pigment layer which backs the photoreceptors is thus

$$18{\cdot}1 - 0{\cdot}2 = 17{\cdot}9 \text{ mm}. \tag{29}$$

The calculated posterior focal length of the schematic eye, equation 28, is 18·0 mm which is close to the distance obtained above for the photoreceptor position from anatomical

considerations. The calculation thus indicates that the schematic eye is nearly emmetropic. The precise refractive error, K, in the schematic eye is given by

$$K = \frac{n_4}{D' - A_1H'} - F = \frac{1{\cdot}337}{(17{\cdot}9 - 4{\cdot}7).10^{-3}} - 100{\cdot}6 = 0{\cdot}7\text{D} \qquad (30)$$

where D' is the distance from A_1 to the photoreceptor layer in mm. The animal is thus found to be only 0·7D hypermetropic—nearly emmetropic.

DUKE-ELDER (1958) describes the wild rabbit as being hypermetropic but suggests that, in captivity, there is a tendency for the animal to become myopic. THOMPSON (1953) found the eye of the anaesthetized rabbit to be about 4D hypermetropic. More extensive investigations of the change in refraction during growth have been conducted by CHOU (1954) and STONE and LEARY (1957). The animals used by Chou were emmetropic after their 40th week while those investigated by Stone and Leary stabilized at about 2D of hypermetropia. The last investigation used British animals. Differences between investigators might result from variations in diets of the animals concerned. GARDINER and MACDONALD (1957) found that a reduction in the protein intake of young rabbits slows their growth and increases their hypermetropia; return to a balanced diet brings about a change towards emmetropia.

The animal population used in the careful investigations of Stone and Leary is likely to be similar to that used in the calculation of the schematic eye. It thus appears that there is at least a 1·3D discrepancy between the observed refractive state and that calculated. It has been pointed out by GLICKSTEIN and MILLODOT (1970) that there is a systematic tendency for smaller eyes to appear hypermetropic because of a difference in the planes of the photoreceptor and light reflection during refraction. On the basis of their calculation an emmetropic rabbit eye should *appear* to be 2D hypermetropic. On this basis the animals examined by Stone and Leary would be emmetropic and the schematic eye predicts a similar state of refraction.

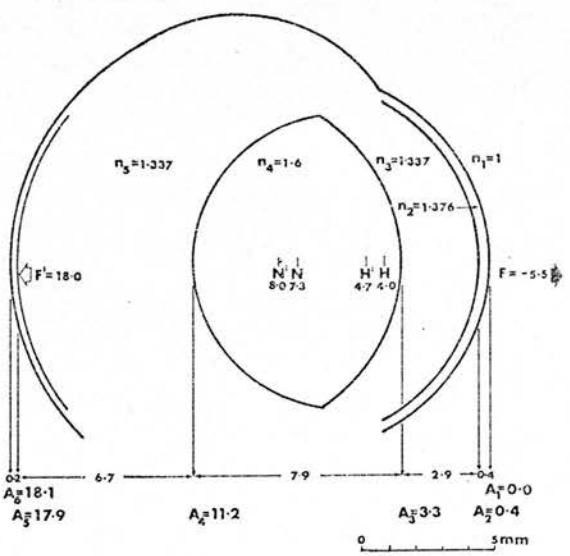


FIG. 1. The main parameters of the rabbit schematic eye in diagrammatic form. Measurements are given in mm from the corneal vertex or between points indicated by arrows. The refractive index of the various media is indicated by a suffixed letter n.

It should be noted that the radius of curvature of the isolated lens anterior surface is in agreement with the value determined by Sorsby *et al.* for the lens *in vivo*. This suggests that the schematic eye represents the lens its state of repose *in vivo*.

The results of the schematic eye calculations are summarised in Table 1 and Fig. 1. A montage of the lens and eye in dorsal view is shown in Fig. 2.

TABLE 1. SCHEMATIC EYE OF THE RABBIT

Refractive Index

Cornea	n_2	1·376
Aqueous and vitreous	n_3 n_5	1·337
Lens (Total index)	n_4	1·6

Dimensions

Surface		Position (mm)	Radius (mm)
Anterior corneal	A_1	0·0	7·5
Posterior corneal	A_2	0·4	7·1
Anterior lenticular	A_3	3·3	6·9
Posterior lenticular	A_4	11·2	−5·8
Receptor	A_5	17·9	—
Posterior scleral	A_6	18·1	−9·8

Powers (D)

	Cornea		Lens		Whole eye	
Anterior surface power	F_1	50·0	F_3	38·0		—
Posterior surface power	F_2	−5·5	F_4	45·0		—
Total power	F_{12}	44·6	L	75·0		100·6

Distances (mm)

Anterior focal length		—		—	f	9·9
Posterior focal length		—		—	f'	−13·3
First principal point	A_1H_{12}	−0·036	A_3H_{34}	3·9	$H_{12}H$	4·0
Second principal point	A_1H_{12}'	−0·44	A_3H_{34}'	3·3	$H_{12}H'$	4·7

Distances from A_1 (mm)

Anterior principal point	H_{12}	−0·036	H_{34}	7·2	H	4·0
Posterior principal point	H_{12}'	−0·44	H_{34}'	7·9	H'	4·7
Anterior focal point		—		—	F	−5·9
Posterior focal point		—		—	F'	18·0
Anterior nodal point		—		—	N	7·3
Posterior nodal point		—		—	N'	8·0

Posterior nodal distance 9·9 mm
Refraction = +0·7D

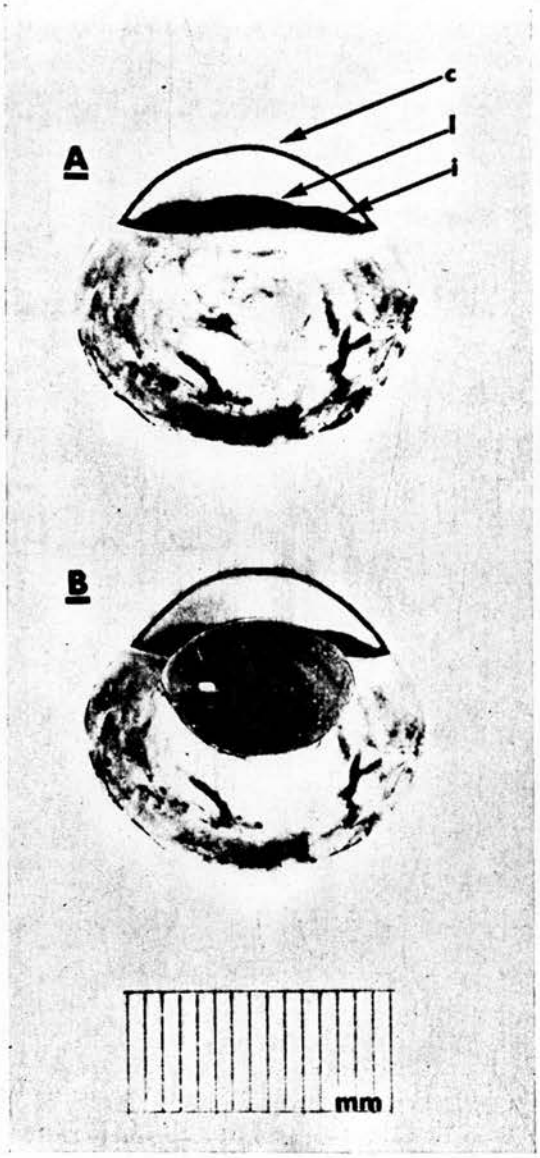


FIG. 2. A. The eye photographed in dorsal view under saline to reveal the cornea, c; lens, l; and iris, i. B. Photomontage showing an excised lens in its correct position in the above eye.

[*facing page* 132

Visual field projection on the retina

The calculation of the retinal arc representing two points one degree apart in the visual field is a necessary preliminary to the examination of the transformation of the visual field projection at various levels in the C.N.S. For this we require a schematic parameter which has not yet been mentioned—the posterior nodal distance.

The eye is an unequifocal system because the refractive index of the first and last media is different. The principal points thus no longer possess the property of being the axial points at which the object and image subtend equal angles. This property now belongs to the axial nodal points. Any paraxial ray incident on the first nodal point will emerge from the system as though from the second nodal point (N') and will be parallel to the incident ray. The positions of the nodal points are simply derived

$$NF = H'F' = f' = -13{\cdot}3 \text{ mm} \tag{1}$$

$$N'F' = HF = f = \quad 9{\cdot}9 \text{ mm}. \tag{2}$$

The latter measurement is the posterior nodal distance which should coincide with the centre of curvature of the retina. The eye in Fig. 1 has a radius of curvature of about 10 mm. Subtracting the thickness of sclera and choroid gives a value of 9·8 mm for the radius of curvature which thus corresponds with the schematic value of 9·9 mm for the PND.

THOMPSON's (1953) measurement of 5·7 mm for the PND of the rabbit appears to be the only directly determined value available in the literature. This figure is considerably different from that predicted by the schematic eye. A measurement of the PND was consequently made on a number of freshly excised eyes inflated to a pressure of 30 cm of water by means of a hypodermic needle inserted into the vitreous and connected to a saline reservoir of adjustable height. Two small light sources 17·4 mm apart and subtending an angle of 10 deg to the eye were placed at a distance of 100 cm and symmetrical about the optic axis. The retinal image of the lights was observed transclerally through a travelling microscope and the chordal distance measured. In this situation it is possible to obtain the PND by similar triangles.

The average of twelve measurements on the equator of the globe and near to the optic axis gave the distance between the images to be 1·7 mm (Av. 12; range 1·5–1·9). The posterior nodal distance is thus given by

$$\frac{1{\cdot}7}{17{\cdot}4} \times 1000 = 9{\cdot}8 \text{ mm} \tag{31}$$

which is in close agreement with the value of 9·9 mm obtained from the schematic eye. It would appear that Thompson may have used a very young rabbit for his measurement.

The observed PND of 9·8 mm means that, in the emmetropic eye, 1 deg in the visual field is represented by

$$\frac{2.\pi.9{\cdot}8}{360} = 0{\cdot}172 \text{ mm} \tag{32}$$

on the retina (assuming the equality of the chordal and circumferential displacements). The schematic eye indicates a figure of 0·173 mm/deg and is in agreement with the observed value.

During the same experiments some observations were made on the retinal representation of the visual field at points away from the optic axis. For at least 45 deg above and below

the equator of the globe the retinal scale was little changed at about 0·17 mm/deg. This value also applied for some 50 deg nasal and temporal along the equator of the globe. At the equator, in the nasal and temporal limits of the field (more than 60 deg out from the optic axis), the value dropped to about 0·15 mm/deg—a change of 12 per cent.

SCHEMATIC VISUAL FIELD

Theoretical monocular field of view

It is possible to use the schematic eye to calculate the limits of the monocular field for an enucleated eye as shown by VAKKUR and BISHOP (1963). A light ray, incident upon the lens, whose extension into the lens intersects the equatorial margin will be refracted into the vitreous humour. Thus, in Fig. 3, the ray A enters at the corneoscleral junction and has an angle of refraction of 20 deg. Assuming that the cornea is a single refracting surface of refractive index 1·38, we find the angle of incidence to be 28 deg. Assuming symmetry of the eye, then this leads to a minimum field of 168 deg. The limit of the field is given by ray B which grazes the lens tangentially and cannot enter. This ray must have an angle of incidence of 50 deg so that the total field must be less than about 212 deg. The actual critical angle depends greatly upon the situation of the lens and pupil relative to each other and the form of the corneo–scleral junction. These factors have not been determined sufficiently accurately for further calculation to be profitable. It suffices that the actual monocular field is the mean of the values suggested above.

Actual unobscured monocular field

The monocular field of view, free of obstruction by the eyelids or body, was determined from measurements of the ophthalmoscopically observed limits of the retinal light reflex of excised eyes centred in a perimeter. During the measurement the eyes were inflated to a pressure of 30 cm/H_2O. The monocular field of the isolated eye was found to extend for 192 deg along the horizontal and 180 deg along the vertical (average of six). This difference of field extent is reflected in the corneal dimensions quoted by DAVIS (1929), of 15·6 mm along the horizontal and 13·8 mm along the vertical. The band of myelinated fibres running from the optic nerve head was used to orientate the eye in its normal position before the measurements were made. The optic nerve head was used as a landmark for reference of the measurements. The horizontal and vertical extent of the monocular unobscured visual field thus lie comfortably within the limits set by the schematic eye calculation.

Actual unobscured whole field

The projection of the optic nerve head into a spherical coordinate system centred on the rabbit's head was determined for 12 animals. This information was then used to nomographically transform the information previously acquired about the unobstructed monocular field so as to construct the real unobscured whole field. The binocular component of the whole field was plotted as though viewed on the front and rear surfaces of a sphere centred on the animals head. The result is shown in Fig. 4a in which the viewpoint lies on an axis passing from the centre of the sphere through the point of intersection of the mid-saggital plane with the nasal region of the equator. The sphere was assumed to be large enough to make the interocular distance negligible. The region of overlap between the monocular left and right fields defines the unobscured binocular field and blind area.

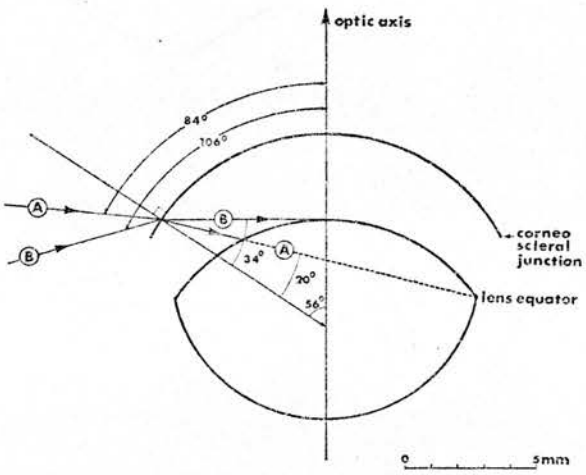


FIG. 3. The limits of the monocular field estimated from the schematic eye. The diagram is explained in the text.

Visual field in vivo

The ophthalmoscopically observed limits of the retinal light reflex were used to determine the total extent of the monocular and binocular fields of view of an intact rabbit in the freeze condition *with its eyelids retracted.* The results are similar to those of PISA (1939) and are shown in Fig. 5 as determined in one characteristic animal. The binocular field begins some 30–40 deg below the horizontal and extends to 70 deg beyond the vertical in the midsaggital plane. The medial intrusion of the monocular field into the opposite half field is at a maximum of 15 deg for each eye in a region directly above the head. The total width of the binocular field is thus not in excess of 30 deg but varies with the action of the retractor bulbi and the position of the eyelids.

The visual field of the rabbit was thus found to be almost a complete sphere. The only totally blind areas are the optic nerve head and the narrow blind sector under and behind the head. The extent of this region is variable and depends upon the body and eyelid positions and upon the length of the animal's fur. The topography of the area is therefore indicated only approximately in Fig. 5 in which the ears are neglected.

For comparison with those of the previous section these results have been plotted in a similar frontal view in Fig. 4a. In the unobscured and actual binocular fields the extent is very similar in the region of the nasal field. The only major difference between them is that the unobscured binocular field is much more extensive to the rear and extends almost to the horizontal; the blind area is thus correspondingly less extensive. This is to be expected as it is in this region that the greatest obscuration of the field by the body occurs. The correspondence between the potential and observed visual fields is clear and indicates that almost all of the field of the eye has been exploited in this much preyed upon animal. This correspondence between the visual field defined by the organisation of the eye and that defined by the marginalia of the orbit may be an important factor in the interpretation of the eye movements of the rabbit and will be taken up in a later publication.

The plane of the iris and of the corneoscleral junction may be seen to be inclined medially at the upper margin by an angle of about 15 deg when observed in an eye *in situ.* This 15 deg

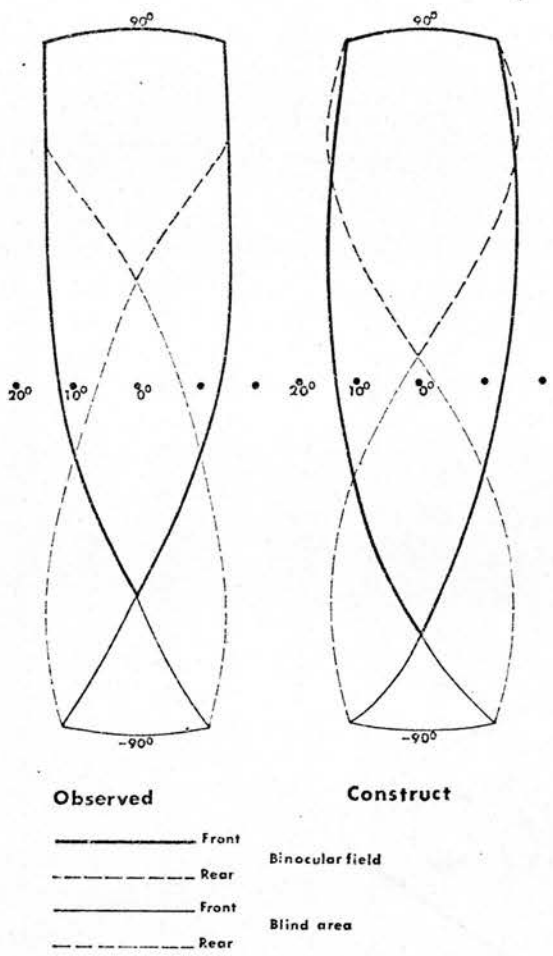


FIG. 4. Measured and constructed potential binocular fields projected onto the surface of a sphere. The viewpoint lies on an axis passing from the centre of the sphere through the point of intersection of the midsaggital plane with nasal region of the equator. See text for explanation.

rotation of the 180 deg vertical monocular field generates the overhead binocular and lower blind areas.

The photographs of the excised rabbit eye shown in Fig. 6 reveal the anatomical basis for the form of the unobscured binocular field in an animal with dilated pupils. Given that the two monocular fields are inclined towards one another by some 15 deg in the vertical, manifested by the large area of iris in the dorsal view (Fig. 6a) compared with the ventral view (Fig. 6c), then the lower nasal binocular field is obtained from the medial extension of the cornea in its lower nasal quadrant. This extension can be seen in the anterior view of the eye (Fig. 6d) as a medial retraction of the corneo-scleral boundary below the equator of the globe. The width of the binocular field in the upper nasal and temporal regions is kept constant by extensions of the cornea in the upper nasal and temporal quadrants. These are indicated by arrows in the dorsal view (Fig. 6a). No extension of the cornea is to be seen in the lower temporal region (Fig. 6b and c) where the blind area coincides with the body.

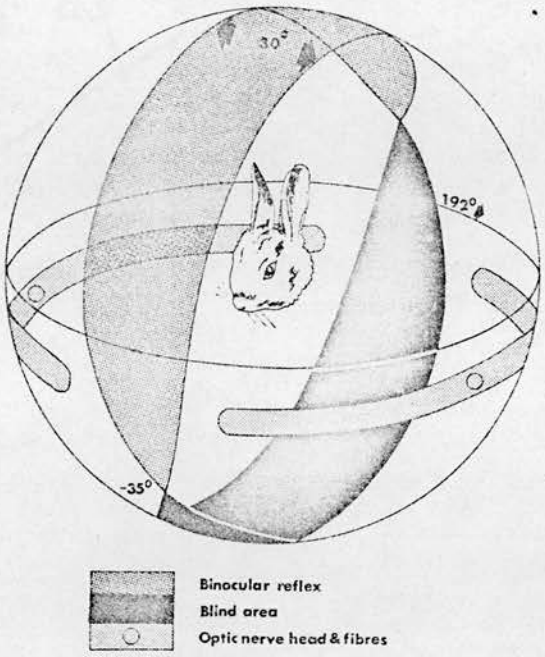


FIG. 5. The visual field of the rabbit divided into its respective binocular, monocular and blind regions. The retractor bulbi are assumed relaxed and the obscuration of field by the ears is ignored.

Figure 6g shows a frontal view of a hare eye which is very similar in organisation to that of the rabbit.

Limit of field to rear of head

The rabbit has been described as possessing a useful binocular field to the rear of the head *on the horizontal*. There seems to be no possibility of this being true; statements to the contrary appear to stem from misinterpretation of Pisa's results (PISA, 1939). His theoretical constructs of the rabbit binocular field show a narrow binocular field within 5 deg of the horizontal but the above findings are in agreement with his observations on the intact animal which suggest that the rear limit of the binocular field is some 30–40 deg above the horizontal. As we have seen that the obstruction of view by extraocular structures forms the main limit to the field of vision at the rear then convergence alone would be inadequate to generate a binocular area at the horizontal level. Even when the head and ears are raised above the level of the body it is not possible to find evidence for the rearward directed binocular field. In Fig. 7 the camera axis is centred on the middle of the rabbit's head and parallel to its long axis. It is possible to see only the corneal vertex of one eye and pupil of neither. As the camera was situated at a distance of three feet from the animal it is possible to show that both pupils should be visible if there is a binocular field of more than 2–3 deg overall. It would have been necessary to move the camera sideways in order to obtain views of either pupil so that it appears that the rear limit to the monocular field runs back almost parallel to the long axis of the body. Ophthalmoscopic observation suggests that it terminates a degree or two lateral to a line parallel to the long axis. The figures presented on page 133 bear out this view. If the monocular overlap into the opposite half field is 12 deg on

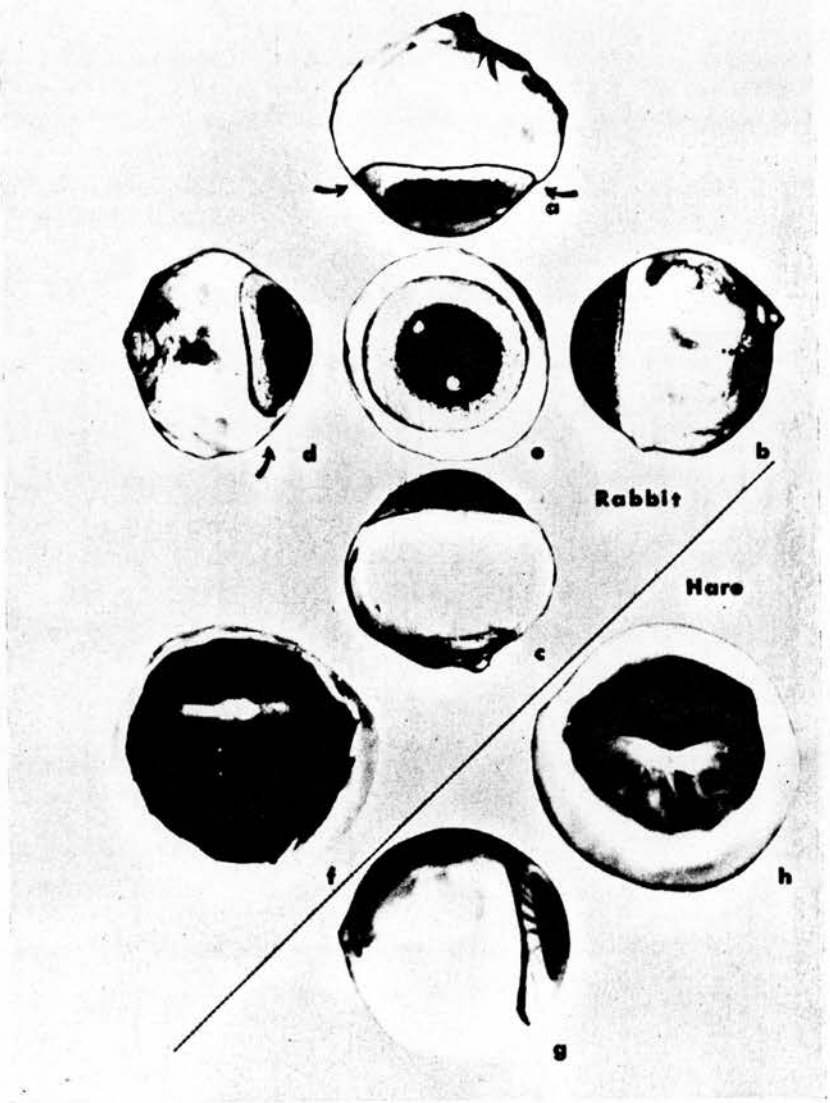


FIG. 6. The excised rabbit eye in dorsal, a; posterior b; ventral, c; anterior, d; and lateral, e, views. In f the eye has been opened to reveal the optic nerve head and myelinated band. Similar views of the hare eye. Anterior view, g; eye opened, h.

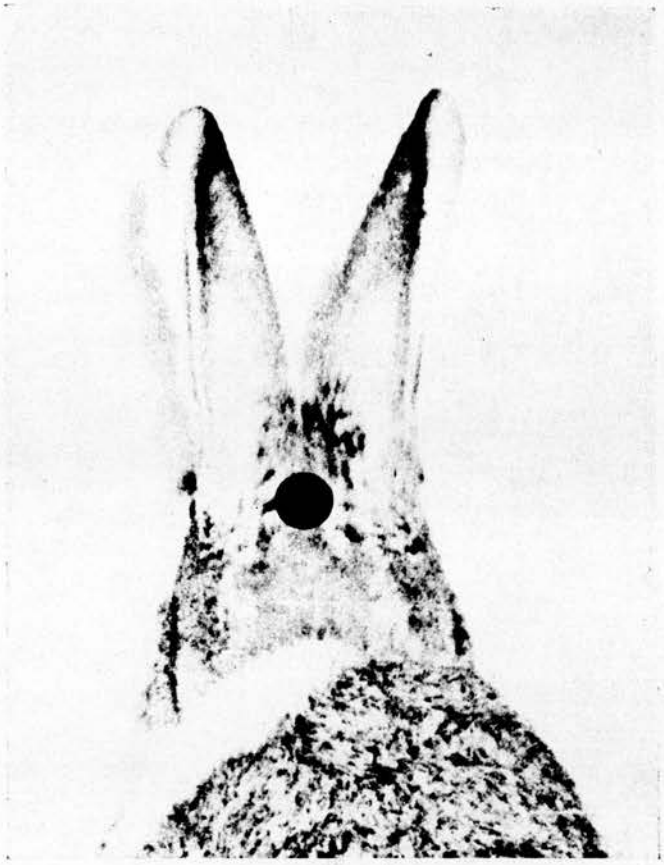


FIG. 7. Photograph taken at a distance of 3 ft showing the absence of a view of the pupils when the camera is centred at the middle of the marked black spot. A binocular field of more than 2 deg could thus not exist.

average then it is clear that with an overall monocular field of 192 deg the rear limit of the field must extend back parallel to the long axis of the head *as long as there is no change in convergence.*

There is, of course, no doubt as to the existence of a binocular field above the level of the horizontal to the rear of an animal in the freeze position.

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VALENTIN (1879). See FREYTAG, G. (1910).

Abstract—A schematic eye has been calculated for the rabbit with measurements made on excised but inflated eyes. The extent of the monocular and binocular visual fields in the intact animal is shown to be nearly as great as is theoretically possible. No binocular field is detectable *on the horizontal* to the rear.

Résumé—On calcule un oeil schématique pour le Lapin à partir de mesures faites sur des yeux énucléés et gonflés. On constate que l'étendue des champs visuels monoculaire et binoculaire sur l'animal intact est presque aussi grande que le permet la théorie. On ne peut pas déceler de champ binoculaire *à l'horizontale* vers l'arrière.

Zusammenfassung—Aus Messung en enukleierten aber luftgefüllten Kaninchenaugen wurde ein schematisches Auge berechnet. Die Grösse des einäugigen und des beidäugigen Gesichtsfeldes des unversehrten Tieres ergab sich als nahezu ebenso gross wie das theoretisch mögliche. Eswar kein rückwärtiges horizontales Gesichtsfeld feststellbar.

Vision Res. Vol. 16, pp. 149–154. Pergamon Press 1976. Printed in Great Britain.

A SUPPLEMENT TO THE CAT SCHEMATIC EYE

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(*Received* 16 *January* 1975)

Abstract—The uniocular and binocular fields of view of the cat eye were calculated by Vakkur and Bishop (1963) from their schematic eye but still lack confirmation by direct measurement. In the schematic eye these authors develop only the fields of view determined by the dioptric apparatus. Their assumption that the extent of the retina is not a limiting factor is shown to be invalid for the cat so that the animal possesses differentiable optical and retinal fields. Measurements supplementary to the cat schematic eye are presented including the requisite extents of the optical and retinal, uniocular and binocular, fields as well as more information about the relative compression of the peripheral retinal image.

INTRODUCTION

The field of view of the dioptric apparatus of the eye has in the past been treated, subject to its restriction by the optic adnexa, as equivalent to that determined by behavioral testing. The long standing assumption that the extent of the retina is not a factor which limits the extent of the behaviourally determinable fields of view was first made explicit by Vakkur and Bishop (1963) when they computed the dioptric uniocular and binocular fields of view from their cat schematic eye. The validity of this assumption and the results of their computations require confirmation by direct measurement. Before proceeding, however, it becomes necessary to define two distinct *uniocular* fields:

The optical field of an eye is the solid angle subtended at its anterior nodal point by that region of space from which light may be refracted through the lens when the eye is free from obstruction by the adnexa.

The retinal field of an eye is that portion of its optical field which is encompassed by the external projection of its retinal margins.

For the animal we may define similar geometrical *cyclopean* (Helmholtz, 1925) fields when the eyes are in the primary position.

The cyclopean optical field of an animal is the solid angle subtended at the cyclopean projection centre by those regions of space from which light may be refracted through the lens of *either* eye when free from obstruction by the optical adnexa.

The cyclopean retinal field of an animal is that portion of its cyclopean optical field which is encompassed by the external projection of the retinal margins of *either* eye.

The binocular field of an animal is that common portion of either the cyclopean optical or retinal fields from which light may be simultaneously refracted through the lens of *both* eyes.

In this paper the discussion of optical and retinal fields is limited to sections, significant in the consideration of binocular vision, through the appropriate solid angles in the presumed plane of fixation (Bishop, Kozak and Vakkur, 1962). The horizontal extent of the cyclopean fields is a function of the distance from which the projection angles of the appropriate delimiting landmarks are ophthalmoscopically determined with respect to the cyclopean projection centre. In the limit, at a measuring distance sufficiently great to make the interocular separation relatively negligible, the cyclopean projection centre and the anterior nodal points of the eyes are effectively coincident. For this situation, which is adopted subsequently in the specification of the angular extent of the cyclopean fields, the angles subtended at the anterior nodal points by the appropriate pairs of nasal or temporal margins of the uniocular optical or retinal fields *of the eyes* may be directly employed to establish the limiting extent of the cyclopean optical, retinal and binocular fields *of the animal* without recourse to further measurement. The cyclopean fields for short distances from the animal require individual computation.

METHODS

A Zeiss Fundus Camera was so mounted that it could be rotated in the horizontal plane about a vertical axis through the centre of its exit and entrance pupils. The axis of rotation was arranged to pass through the anterior nodal point of the eye of an anaesthetised and paralysed cat. The orientation of the camera about its axis of rotation was measured by a vernier protractor; in conjunction with the ocular cross hairs the projection of the fundus landmarks could be determined repeatably within ±0·1°.

Threads were sutured to the eye just in front of the insertions of the lateral recti in order to enable its horizontal rotation to arbitrary positions in which the fundus camera had access to the limits of the field on one side or the other.

The retinal magnification and P.N.D. were also determined with this apparatus. The angles subtended between conspicuous blood vessel intersections or tapetal features which projected into the visual field close to the equator were measured with the fundus camera in regions of temporal, nasal and central retina. The corresponding distance between these landmarks was subsequently measured on the flattened cup of the eye by means of a dissecting microscope equipped with a vernier eyepiece. The retinal magnification is obtained as the quotient of the two measurements for a given pair of landmarks.

A contact lens was not fitted to the eye during any of these measurements. The cornea was maintained clear by a saline drip when the pupil had been dilated.

The internal geometry of the cat eye was examined in enucleated and frozen globes. After enucleation the eye was connected to a pressure source of 20 cm of saline by means of a hypodermic needle and subsequently arranged on the stage of a freezing microtome so that the plane of the posterior ciliary vessels was horizontal. The upper half of the eye was removed to the level of the optic nerve head after freezing had occurred. The cut surface appeared as in Fig. 3(a) and was photographed at known magnification with the retinal margins indicated by markers.

RESULTS

The projection of the retinal landmarks into the uniocular field of the cat eye

The angular projections with respect to the optic nerve head of:

(1) the limits of the optical field of the eye (the ciliary processes which appear like black "arrowheads" pointing into the vitreal cavity cease to be visible);

(2) the transition from the pars plana to the pars plicata of the ciliary body (the pars plana of the nasal retina is observable only with a fine ophthalmoscope beam);

(3) the retinal margin in the plane of the optic nerve head (visible as a fine vertical line at which the retinal reflex changes colour to a dark orange at the ciliary body);

(4) the vertical tapetal margin in the plane of the optic nerve head;

were measured in the presumed fixation plane for the nasal and temporal field of one eye in each of 10 cats of mean weight 3·5 kg (range 2·8–4·2 kg). The results of these observations are summarised in Table 1 and Fig. 1 as if for the left eye. The projection of the various features was subsequently referred to the area centralis by assuming the angle 14·5° (αB, $n = 40$; Bishop *et al.*, 1962a) to be the horizontal angular separation of the presumed visual pole from the perpendicular projection of the optic nerve head into the plane of fixation when the eye is in the position of paralysis. The results in Fig. 1 are presented according to both conventions.

The unobstructed optical field of the cat eye was found to have a mean horizontal extent of 181°, Fig. 1, but *of this angle only the* 143° *which are served by the retina* (*Fig.* 1) *are to be regarded as contributing to the behavioural field of the cat.*

The limits of the optical field of the eye and the zonular fibre insertions into the ciliary processes, are all symmetrically disposed about the optic nerve head; by contrast, the retinal margins lie on average 65° nasal and 79° temporal of the blind spot with the consequence that the width of the ciliary body must be naso-temporally asymmetric in complementary fashion to the retina. This is readily observed in the flattened eye cup of Fig. 2.

A noticeable feature of the cat ciliary body is that it is divided into two parts, as in the human eye, a pars plana bearing the ciliary processes and the valleys between them, which separates the retina from the pars plicata. The width of the pars plicata is quite constant but this is not true for the pars plana. In the temporal eye cup, where the retina is least extensive, the pars plana is of 3·7 mm mean width and subtends an angle of 20° in the nasal field (Fig. 1). On the nasal side of the cup the pars plana is less than 0·5 mm wide and subtends about 2° in the temporal visual field. The naso-temporal asymmetry in width of the ciliary body is thus located in the pars plana. The 181°–143° = 38° mean blind area of the uniocular optical field, which corresponds to the projection of the ciliary body, thus has its largest segment, 26°, projecting into the nasal field where it is masked by the nose. The remaining 12° projects to the extreme temporal field and appears to be reduced when the pupil is constricted.

The asymmetry of the retinal margins is more pronounced when their projection is referred to the area centralis; the nasal margin then projects, on average, 94° temporal in the field and the temporal margin some 49° nasal, which corresponds well to the position of the bridge of the nose. The cat eye thus has little or no reserve of retina projecting behind the nose and reduction in the extent of the binocular field must develop during even modest versions of the eyes.

Table 1. The projection of the retinal landmarks into the uniocular field of the cat eye

	Landmark	Mean angle subtended at the A.N.P. with respect to O.N.H. Degrees	S.D. Degrees	to A.C. Degrees
TEMPORAL FIELD	Limit of the optical field	90.8	3.52	105.3
	Pars plana/pars plicata border Ora terminalis	78.8	3.01	93.3
	Tapetal margin	49.8	7.64	64.3
	Optic nerve head (O.N.H.)	00.0		14.5
	Area centralis (after Bishop et al., 1962; A.C.)	14.5	1.86	00.0
	Tapetal margin	56.2	1.88	41.7
	Ora terminalis	63.9	3.82	49.4
	Pars plicata/pars plana border	81.6	2.52	67.1
NASAL FIELD	Limit of the optical field	90.1	1.6	75.6

Uniocular optical field	180.9 ± 3.87°
" retinal field	142.7 ± 4.86°
Cyclopean optical field	210.6°
" retinal field	186.6°
Absolute binocular field	98.8°

n=10. Mean weight 3.45 Kg (range 2.8 - 4.2 Kg).

All measurements are in a plane close to the presumed fixation plane.

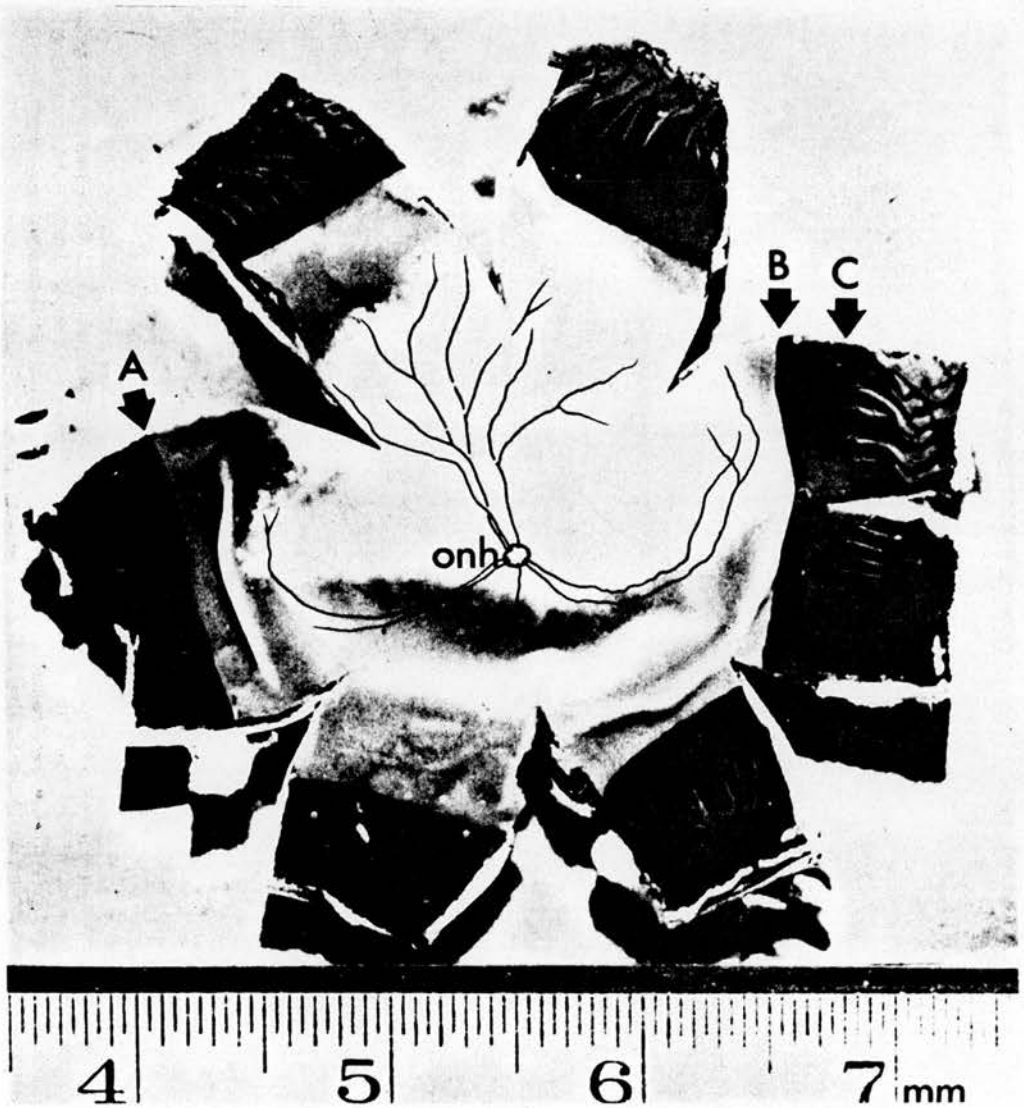

Fig. 2. The open, flattened cup of a cat left eye showing the relative extents of the retina and ciliary body. On the nasal side, A, the pars plana of the ciliary body is very narrow but it is considerably wider in the temporal cup, B–C, where the corresponding optical field is screened off by the nose.

[*facing page* 150

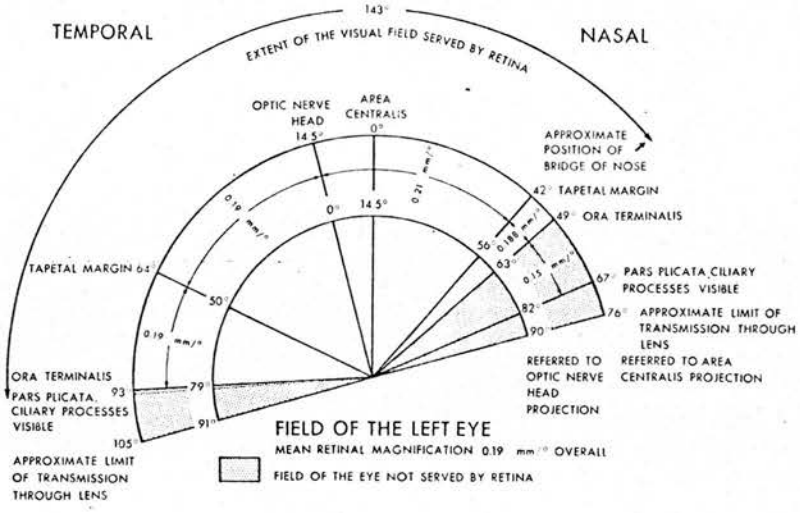

Fig. 1. The visual field of the left eye of a cat showing the extent of the uniocular retinal and optical fields as well as the angular projection subtended at the anterior nodal point (A.N.P.) of various retinal landmarks referred to both the area centralis and the optic nerve head. The grey area indicates the sectors of the optical field which are not served by the retina. The greater part of this blind field projects behind the nose. The mean retinal magnification factors at various eccentricities are entered in the appropriate sectors. The angular projection of the area centralis was obtained from the literature (see text) but the other projections were measured in one eye from each of ten cats and represent mean values for which more details are to be found in Table 1.

In Fig. 2 it is worthy of note that the margin of the cat retina is free of dentate processes so that its common description as the ora serrata is quite inappropriate and should be replaced by the phrase ora terminalis.

The extent of the cat cyclopean field of view in the presumed plane of fixation

When the eyes are in the primary position the left and right 105° temporal optical hemifields, Fig. 1, sum to generate the 211° cyclopean optical field of the cat. Under the same conditions the nasal ora terminalis of each retina delimits the mean 93° temporal retinal hemifields and defines the 187° mean extent of the cyclopean retinal field of the cat. The cyclopean optical field of the cat thus exceeds the corresponding retinal field by the two 12° sectors which project onto the ciliary body and is of little functional interest; it is the cyclopean retinal field which determines the extent of the animal's ability to detect visual stimuli.

The absolute binocular fields of the cat are defined by the angle between the nasal margins of the right and left optical or retinal fields. Only the binocular retinal field is of interest; it extends for some 99°. The nose of the cat obscures little of this retinal field and thus the adnexa restricted (relative) retinal binocular field is only slightly smaller than the absolute field. The monocular crescents of the cyclopean retinal field extend for (187°–99°)/2 = 44° and are illustrated with the other fields in Fig. 3.

The cyclopean field magnitudes are critically dependent upon the value chosen to represent the angle αB, the mean separation in the plane of fixation of the optic nerve head projection from the visual pole; an error in this angle is doubled in the cyclopean fields. The value of 14·5° (Bishop *et al.*, 1962a) employed in this paper for the angle αB is, however, amply confirmed by the mean of 14·3° obtained from a larger sample (Hammond, $n = 90$; personal communication) and two independent non-ophthalmoscopic means of 14·8° (Sanderson, 1971).

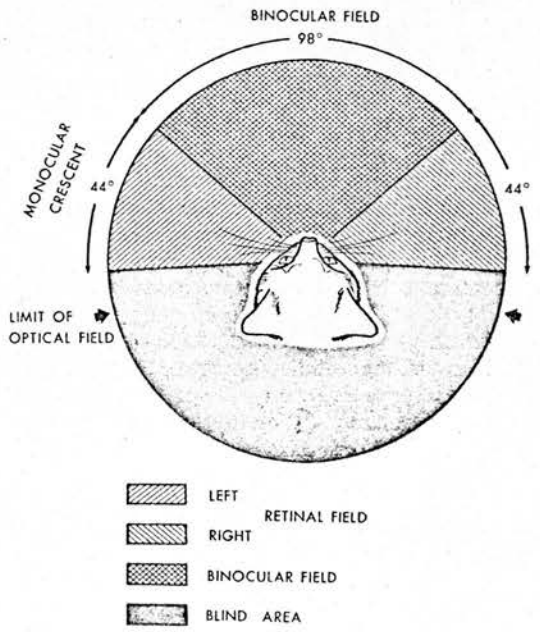

Fig. 3. The extent of the monocular crescents and binocular field of the cat as constructed from the measured *retinal* uniocular field described in Fig. 1. It is assumed that the visual axes are parallel and that the separation of the eyes is insignificant at the distance from which the measurements of the angular limits of the field are made. This diagram may be compared with the results of behavioural perimetry (Sherman, 1973) but not with estimates of the *optical* limits of the field. The influence of the bridge of the nose in limiting the extent of the binocular field has been neglected.

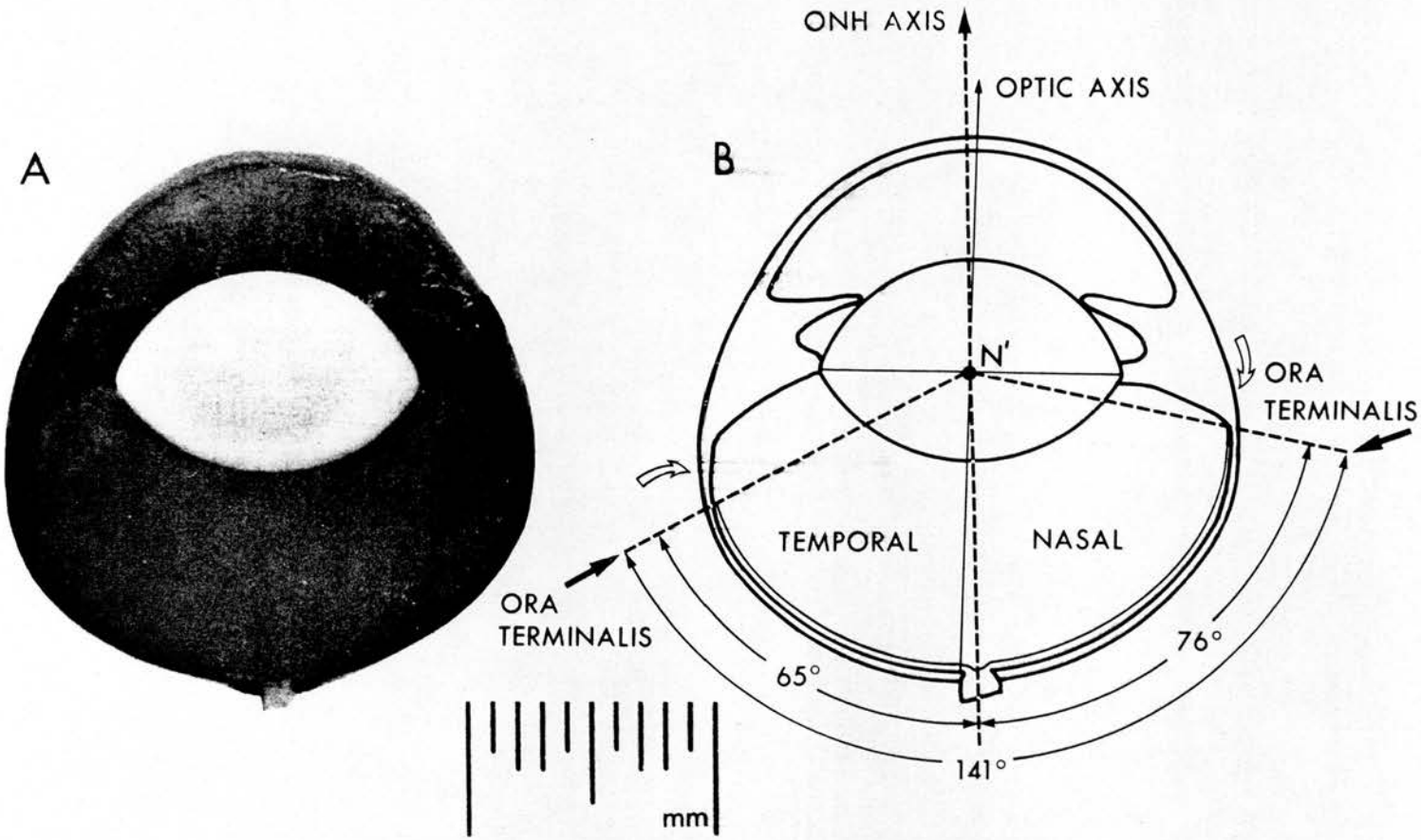

Fig. 4. A frozen section of the right eye of a cat, A, upon which markers indicated the ora terminalis and enabled the angle subtended by the retinal margins at the schematic posterior nodal point, N′, to be determined, B. The optic axis is defined as the bisector of the corneal base and the lens equator; it projects 2° temporal of the optic nerve head centre in this superior view and is approximated in the diagram by the optic nerve head axis. The plane of the section passes through the optic nerve head parallel to the posterior ciliary vessels. The open arrows indicate thickening of the posterior wall which presumably defines the limit of transcleral illumination beyond the retinal margin.

On the internal retinal field of the cat's eye

The angular extent of the externally projected retinal field is thus established to be 142° subtended at the anterior nodal point in the horizontal plane. If the angular transformations of the cat optical system are linear then the retinal margins would internally subtend the same angle at the posterior nodal point.

The internal geometry of the cat eye was examined on photographs of enucleated globes which had been frozen with the posterior ciliary vessels in the horizontal plane and sectioned to the level of the optic nerve head. The appearance of such a section is shown in Fig. 4 which is characteristic of the other eyes.

The optic axis, defined by the perpendicular bisector of the corneal base and lens equator intersected the eye cup consistently at an angle of some 2° nasal of the optic nerve head in agreement with the findings of Bishop *et al.* (1962a). For measurement purposes this axis was approximated by the projection line of the optic nerve head through the lens centre. The posterior nodal point position was entered on this axis at the appropriate proportional distance of 0·42 of the antero-posterior dimension of the eye specified by the cat schematic eye (Vakkur and Bishop, 1963). The point so defined was close to the midpoint of the lens equatorial diameter and to the centre of curvature of the surface defined by the inner limiting membrane. The angles subtended at this approximated posterior nodal point by the retinal margins were measured on the photographs of one eye from each of four cats weighing a mean 3·3 kg (2·9–3·5 kg). The results are incorporated in Table 2.

The relative and absolute extents of the nasal and temporal visual hemifields are thus seen to be of very similar magnitude to their corresponding internal fields subtended at the posterior nodal point. The total internal and external retinal fields of 139° ± 2·1° and 143° ± 4·9° respectively are not significantly different.

The results suggest that the retinal image of the cat is a relatively good central projection of the external world with a linear transformation from angles subtended by external objects at the anterior nodal point to those subtended by their images at the posterior nodal point. It should be remembered that the nodal point of the schematic eye is defined for axial rays alone and it does not follow that a linear angular transformation will apply for peripheral rays. Measurement of the retinal magnification factor at various eccentricities is required to elucidate this point.

The retinal magnification factor and P.N.D.

The posterior nodal distance (P.N.D.; the separation of the posterior nodal point from the posterior focal point) of one cat eye was reported by Vakkur *et al.* (1963) to be constant at 13 mm (a retinal magnification factor (RMF) of 0·227 mm/deg) over an 80° central sector but to drop to 11·5 mm (RMF of 0·20 mm/deg) in the extreme periphery. These results were obtained from eyes equipped with contact lenses which have been shown (Vakkur *et al.*, 1963) to increase the effective PND, even if of zero power, and to distort the projection of the peripheral field. The alleged peripheral reduction of PND and RMF thus requires confirmation in eyes free from contact lenses.

Central and peripheral determinations of the RMF were made with a fundus camera according to the technique described in the Methods section and the following mean values obtained:

Central RMF	0·21 mm/deg	($n = 5$)
	(range 0·205–0·22 mm/deg)	
Peripheral RMF; 60°–70° nasal or temporal of ONH	0·17 mm/deg	($n = 10$)
	(range 0·15–0·18 mm/deg).	

The high accuracy of angular measurement ±0·1°, and distances, about ±0·05 mm, indicates that the difference between central and peripheral magnification factors can be taken as significant for this sample.

It is, however, questionable as to whether measurements made on the somewhat elastic strip of the retina represent the equivalent dimensions in the globe at some 20 cm of water pressure. The mean separation of the nasal and temporal ora terminalis (retinal length) in four eyes frozen at an internal pressure of 20 cm of water and sectioned parallel to

Table 2. Internal geometry of the cat eye

	Landmark	Mean angle subtended at the P.N.P. with respect to O.N.H. Degrees	S.D. ± Degrees	% age of retinal field. Degrees
NASAL RETINA	Ora terminalis	76.5 (78.8)	1.87	55% (55%)
	Optic nerve head	00.0		
TEMPORAL RETINA	Ora terminalis	62.8 (63.9)	0.93	45% (45%)
Internal retinal field	$\overline{139.3°} \pm 2.09°$ (142.7°)			
$\overline{A_1A_6}$	21.6 mm			
$\overline{AN'}$	9.08 mm			
$\overline{P.N.D.}$	12.2 mm			

n=4. Mean weight 3.27 Kg (range 2.9 - 3.5 Kg).
Angles in parentheses indicate the magnitude of the equivalent external angle subtended at the anterior nodal point (A.N.P.) and are from Table I.

the posterior ciliary vessels in the plane of the optic nerve head was consequently measured and found to be 29·0 ± 0·65 mm (mean weight of animals, 3·27 kg). The vitreous expands upon freezing with a specific volume change from 1·0 to 1·09 cm^3/g; the circumference of the eye thus increases by a factor of 1·03. The mean 29-mm-long frozen retina corresponds to a 29/1·03 = 28·2 mm retina in the intact eye of the cat at body temperature. The mean length of five excised retinas, of which four were from the companion eyes to those frozen, was 28·25 ± 0·8 mm which is in close agreement with the measurements from the frozen eye corrected for expansion and suggests that the *in situ* retinal dimensions are well represented by measurements on the excised tissue.

This finding justifies the use of another estimate of the mean RMF values at various eccentricities. The separation of the various landmarks recorded in Table 1 was measured on the pinned-out equatorial strip of eight eye cups untreated with fixative; the retina remained attached to the ciliary body. The RMF values presented in Table 3 were calculated as the quotient of a given mean landmark separation with the mean angle recorded in Table 2 as subtended between these features at the anterior nodal point. From these results we obtain the *average retinal magnification as* 0·198 mm/deg *overall.*

retinal fields may thus be greater in animals with frontal than in those with lateral eyes.

Previous measurements of the extent of the optical fields have most commonly been made by means of the unreliable technique of transcleral illumination rather than by direct examination of the fundus reflex. This method has suggested the cat uniocular optical field to be from 150° (Vakkur and Bishop, 1963) to 200° (Thieulin, 1927) in extent and defines neither the retinal nor optical fields measured from the fundus reflex. The extent of the field established by transcleral illumination must be a complex function of scleral thickening, pigmentation and intensity of the light employed. The 181° uniocular optical field reported above was, however, well bridged by the range of 158°–214° calculated from the cat schematic eye (Vakkur and Bishop, 1963).

At least a 90° sector of the cat uniocular field of view temporal of the visual axis projection is represented in maps obtained electrophysiologically from the LGN (Seneviratne, 1963; Bishop, Kozak, Levick and Vakkur, 1962b) and superior colliculus (Vejbasesya, 1967). This value is confirmed by the mean 93° temporal extent of the retinal field of the eye in Fig. 1. No estimate of the nasal limit of the central representation of the field of view of one eye

Table 3. Estimated *in situ* retinal magnification factor

		Mean angle in field rel. ONH (Table 1)	Mean sector width in field	Mean sector width on excised retina		Mean RMF for sector	Sector mid point rel. ONH
		Degrees	Degrees	mm.	S.D. ± m.	mm/°	Degrees
TEMPORAL FIELD	Limit of the optical field	90.8	12.0	-	-	-	-
NASAL RETINA	Pars plana/pars plicata border	78.8	29.0	5.52	0.93	0.190	64.3
	Ora terminalis	49.8	49.8	9.68	1.18	0.194	24.9
	Tapetal margin	00.0	56.2	11.64	0.8	0.207	28.1
	Optic nerve head	56.2	7.7	1.41	0.3	0.183	60.0
TEMPORAL RETINA	Ora terminalis	63.9	17.7	2.73	0.51	0.154	72.8
	Pars plana/pars plicata border	81.6	8.5	-	-	-	-
NASAL FIELD	Limit of the optical field	90.1	-	-	-	-	-
		(n=10)	(n=10)	(n=8)			

(Average RMF 0.198 mm/° overall.)

DISCUSSION

The uniocular field

The optical field of the cat eye is reported above to exceed the uniocular retinal field by 38°, a substantial difference which is sufficient to call into question those estimates of the behavioural fields of other species which have been based upon measurements of their optical fields. Examination of frozen sections of the rabbit eye (unpublished observations) suggests that its behavioural 360° panoramic field with binocular overlap requires the use of the entire uniocular optical field by the retina and that in this animal the optical fields may indeed suffice to indicate the extent of the retinal and behavioural fields. The discrepancy between the optical and free from obstruction by the nose appears to be available in the literature. An eccentricity of some 50° would be expected from Fig. 1.

The cyclopean fields of view

The 211° extent of the cyclopean optical field of the cat which is reported above is close to the estimate of 200° given by Vakkur and Bishop (1963) but considerably smaller than the 290° of Thieulin (1927) or the 280° of Duke-Elder (1958); the great extent of the latter fields arises from the false assumption that the nasal limit of the uniocular field coincides with the bridge of the nose. The mean 211° cyclopean optical field is served by a retinal field extending only 187° which is more restricted than the

208° over which a behavioural response can be elicited in man (Hartridge, 1919).

When the eyes are in the primary position the blind sector to the rear of the cat's head extends for some 173°; this is made up of 24° of retina free optical field and 149° of non-optical field. The blind sector is thus considerably in excess of the 80° claimed by Thieulin (1927) and Duke-Elder (1958).

The absolute binocular optical field of the cat was calculated to extend for 140° by Vakkur and Bishop (1963); measurement indicates a mean value of 151° ($n = 10$). The *retinal* binocular fields are, however, of greater significance. The absolute and relative binocular retinal fields are concluded to differ little in the cat and the 99° absolute binocular retinal field is taken to represent them both; it is much smaller than the restricted field of man.

Behavioural food perimetry with conscious cats offers a means of confirming the measurements of the retinal monocular and binocular fields. According to Sprague and Meikle (1965) and Sherman (1973) the lateral limit of the behaviourally determined cyclopean field of the cat lies about 100° temporal of the fixation axis rather than the 93·3 ± 2·15° (95%) reported above. The behavioural unicocular field extended for 145° (143° above) and the nasal monocular hemifield for 45° (49° above). The agreement between the two estimates is quite good but it should be noted that the perimetry technique does not prevent small eye movements.

The retinal magnification factor

The mean peripheral RMF value for the tapetal-free nasal and temporal sectors in the pooled measurements of Table 3 is 0·187 mm/deg at an average eccentricity of 62°; a similar proportional reduction relative to the central value to that reported by Vakkur *et al.* (1963). The undoubtedly significant central and peripheral means of the individually computed RMF values (p. 154) indicate a smaller peripheral value of 0·17 mm/deg and a larger proportional difference. The latter observations were commonly made at greater eccentricities than the average 62° of the former which accounts for their lower value. In the temporal eye cup at such larger eccentricities the RMF across the pars plana, midpoint 72·3° from the ONH, is as low as 0·158 mm/deg (Table 3).

The largest RMF of Table 3, 0·207 mm/deg, is attributed to the 56° sector which contains the area centralis. The value appears to be even greater between the area centralis and the ONH. Direct measurement of the angular separation, ωB, of the optic nerve head, B, from the ophthalmoscopically estimated geometrical centre of the area centralis, F, (Bishop *et al.*, 1962a; Vakkur *et al.*, 1963) gives a pooled value of $\omega B = 15{\cdot}98°$ ($n = 50$) which is confirmed by a larger sample in which $\omega B = 15{\cdot}7°$ ($n = 90$) (Hammond, personal communication). From Hughes (1975) we have the mean separation of the optic nerve head from the peak count of the area centralis as 3·4 ± 0·16 mm ($n = 22$) in the unfixed preparation. The central retinal magnification factor is thus computed to be 0·213 mm/deg in the immediate vicinity of the area centralis and ONH compared with 0·218 mm/deg derivable from the cat schematic eye (Vakkur *et al.*, 1963).

Even the averaged peripheral reduction of RMF in Table 3 indicates that an error of up to 12% will result from the conversion of peripheral retinal *distances* into angular separations when a single conversion factor appropriate to the central retina is employed (Stone, 1965) The use of the central factor for the computation of the solid angle subtended by an *area* of peripheral retina (Stone, 1965) will result in its underestimation beyond the tapetal margins by 22% or more in regions closer to the ora terminalis. We thus find the deviations from a central projection (p. 152) to be quite substantial in the peripheral field.

Acknowledgements—I wish to thank A. Goodwin and G. Henry for permitting measurements to be made on their cats and P. Hammond for access to unpublished optical data. It is a pleasure to acknowledge the secretarial assistance of Ms. L. Speight.

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Vision Research Vol. 19, pp. 1273 to 1275
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0042-6989/79/1101-1273$02.00/0

RESEARCH NOTE

A USEFUL TABLE OF REDUCED SCHEMATIC EYES FOR VERTEBRATES WHICH INCLUDES COMPUTED LONGITUDINAL CHROMATIC ABERRATIONS

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(*Received* 29 *December* 1978; *in revised form* 1 *March* 1979)

A schematic eye in which the dioptric apparatus has been replaced by a single refracting surface which separates air from water is a very simple and useful tool in a variety of optical calculations. Several such "reduced" model eyes for man have been based on the full schematic eye developed by Gullstrand (1909). Now that complete schematic eyes have been calculted for a variety of vertebrates it is possible to employ their parameters to generate the more convenient reduced models.

The reduced eyes presented in Table 1 are developed from the published dimensions and parameters of the full schematic eyes which are conveniently summarized in Table 1 of Hughes (1977) where a bibliography of source papers is provided for a variety of species. The power, P_D, of the reduced eyes for yellow light of the D line, $\lambda = 589\ m\mu$, was equated with the reciprocal of the anterior focal length of the full schematic eye, HF. The posterior focal length of the reduced, water filled eye is then $1.3330 \cdot HF$ for yellow light. The single principal point of the reduced eye was placed at the same distance, AH, behind the corneal vertex, A, as the anterior principal point of the full schematic eye. The length of the reduced eye is given as the sum of AH and HF' of Table 1 and defines the position of the effective image plane of the retina for emmetropia. The modulus of the anterior focal length is equal to the posterior nodal distance, $|HF| = NF'$, so that the nodal point position is defined and the size, S, of the retinal image of an object subtending an angle α is given by $S = HF \cdot \tan \alpha$.

The radius of curvature, RC, of the refracting surface of the reduced eye, situated at H on axis, is thus defined as HN or may be computed as $RC = (n_{air} - n_{water})/P_D$. This latter formula was then employed to obtain the power of the eye for red light, C line with $\lambda = 656\ m\mu$, and blue light, F line with $\lambda = 486\ m\mu$, from the published values for the dispersion of water at 20°C (Fowle, 1934) at these wavelengths; the radius of curvature of the refractive surface was held constant. The temperature chosen was considered representative of conditions under which most schematic eye measurements have been made on enucleated globes. A generalized diagram, Fig. 1, indicates the significance of the various parameters of the reduced eye.

If the separation of the second principal point, H', and the effective image plane of the retina is denoted by $H'E$, the longitudinal refractive error by R and the power of the refracting surface by P, then for 'X' line light we may write $n_X/H'E = P_X + R_X$. If $H'E$ is kept constant and the system is emmetropic for D line light, so that $R_D = 0$, then subtracting the relationship for X line light from that for D line light gives the longitudinal chromatic difference, or aberration, as $R_{D-X} = -P_D + P_X(n_D/n_X)$ (Le Grand, 1967); this value is tabulated for C and F line light in Table 1 along with the corresponding whole eye powers. The change in refractive index with wavelength alters not only the optical power but also the optical length of the system image space, $n_X/H'E$, in such a way as to ensure that the longitudinal aberration is always smaller than the difference in whole eye powers.

The refractive indices for the ocular humors appear to be in fact somewhat higher than for water and the range of dispersion about 25% greater, but the available information is limited; Le Grand (1967) lists a few sources and Nakao *et al.* (1968) tabulate dispersion information for the rabbit eye media. The computed parameters of the models are similar in magnitude to those of the full schematic eyes with the greatest deviations in the reduced parameters arising from the use of a single principal point in species whose homogeneous-lens model eye has widely separated

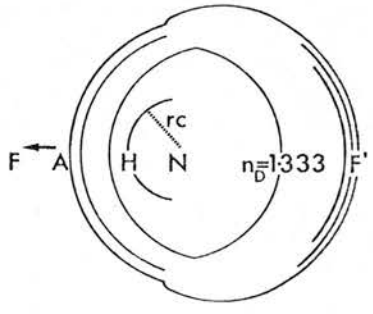

Fig. 1. The outline of a reduced schematic eye. A, corneal vertex; H, principal point and position of the refraction interface between air and water of refractive index 1.333; N, nodal point; RC, radius of curvature of the refracting surface; F and F', the anterior and posterior focal points.

Table 1. Parameters of reduced schematic eyes for vertebrates*

20°C	$\lambda = 589\ m\mu$ $n_D = 1.3330$						$\lambda = 656\ m\mu$ $n_C = 1.3312$	$\lambda = 486\ m\mu$ $n_F = 1.3371$	Longitudinal chromatic aberration	
	AH (mm)	*AN* (mm)	*HF* (mm)	*HF'* (mm)	Radius curv. (mm)	P_D (D)	P_C (D)	P_F (D)	R_{C-D} (D)	R_{F-D} (D)
Man	1.348	7.027	−17.055	22.734	5.679	58.634	58.320	59.359	−0.235	0.543
Macaque	1.523	5.539	−12.060	16.076	4.016	82.919	82.470	83.939	−0.338	0.762
Cat	4.514	8.784	−12.823	17.093	4.270	77.986	77.564	78.946	−0.316	0.719
Rabbit	4.000	7.297	−9.900	13.197	3.297	101.010	100.455	102.245	−0.419	0.921
Rat	1.651	2.759	−3.326	4.434	1.108	300.661	299.036	304.363	−1.222	2.767
Pigeon	0.760	3.394	−7.910	10.544	2.634	126.422	125.740	127.980	−0.515	1.165
Frog	2.290	3.649	−4.080	5.439	1.359	245.098	243.780	248.123	−0.988	2.263
									Hypermetropia	Myopia

A—Corneal vertex.
H—Principal point and position of refracting surface.
N—Nodal point.
F—Anterior focal point.
F'—Posterior focal point.
RC—Radius of curvature of refracting surface.
P_X—Power of whole eye model for '*X*'-line light (where '*X*' stands for *D*, *C* or *F*).
R_{X-D}—Difference in focus for '*X*' and *D* line light expressed in diopters, i.e. the longitudinal chromatic aberration and *not* equal to $P_X - P_D$.
n_X—Refractive index of water at 20°C for '*X*' line light (*D*, *C* or *F*).
D—Diopters.
D, C, F—Subscript; parameter value for light of corresponding spectral line.
|*HF*|—Is of the same magnitude as the posterior nodal distance.
* Three figure accuracy is not implied.

principal points. The computation must be carried through according to the above schema to six figures accuracy in order to achieve consistency with the tabulated values which are rounded to three figures.

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Vision Research Vol. 21, pp. 1129 to 1148, 1981
Printed in Great Britain

0042-6989/81/071129-20$02.00/0
Pergamon Press Ltd

AN ANALYTIC, GRADIENT INDEX SCHEMATIC LENS AND EYE FOR THE RAT WHICH PREDICTS ABERRATIONS FOR FINITE PUPILS

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(*Received* 18 *July* 1980)

Abstract—Schematic eyes with a homogeneous equivalent lens are inadequate for non-paraxial optics and available versions have been invalidly fitted to non-paraxial properties.

A new model eye is here analytically derived from the refractive index profile of the crystalline lens and anatomical measurements of the rat eye. It predicts spherical abberration, coma, paraxial properties and the variation of refractive state with pupil size in accord with experimental measurements.

The cornea counteracts the spherical aberration and linear coma of the lens so that overall aberration is reduced and the eye is of good optical quality. *The nodal point is invariant with object eccentricity* in a manner advantageous to a species whose visual axis is displaced from the optic axis. The potential of the model lies in its extension to a study of such off-axis optics.

INTRODUCTION

The authors of many schematic eye models (see Hughes, 1977b) follow Vakkur and Bishop (1963) and substitute a homogeneous lens of uniform fictitious refractive index for the non-uniform, *gradient index* distribution of the crystalline lens. This uniform, *total index* is pragmatically determined from the measured back vertex power of the real lens but the power and cardinal point positions so obtained may not be correct. Indeed, such homogeneous lenses appear to be inferior to Gullstrand's (1924) core model which he claims to accurately locate the principal points of the lens.

The excessive separation of the principal planes in homogeneous lens models may introduce significant error into the computed optical state; Hughes (1979a) approximated their true positions by employing a two shell model for the rat lens. But, like models based on homogeneous lenses, his rat schematic eye employs Gaussian approximations and can deal only with paraxial optics.

More general, non-paraxial, schematic eyes have been essayed for man. Pomerantzeff *et al.* (1971), employ some 96 parameters to define the form of the index gradient and isoindicial surfaces. Even a fit of the model to measured spherical aberration required manipulation of eleven of these parameters. The resulting solution may not be unique and the degree to which it approximates reality, or predicts properties other than spherical aberration is unclear. Lotmar (1971) ignored the refractive index gradient and employed aspheric lens and cornea surfaces to fit his human schematic eye to measured spherical aberration but he failed to predict observed astigmatism (Rempt *et al.*, 1971; Lotmar and Lotmar, 1974).

The refractive index profiles of crystalline lenses have been measured and employed to compute schematic eyes for the rabbit (Nakao *et al.*, 1968), monkey and human (Nakao *et al.*, 1970). Discrete isoindicial shells were used to approximate the measured continuous distribution of refractive index with possible detriment, at great obliquity, to the accuracy of the ray traces. No attempt was made to check the predictions of these models against measured optical properties. The predicted power of the rabbit lens is not in agreement with that measured directly (Hughes, 1972; Ludlam and Twarowski, 1973).

Philipson's (1969) measurements of the gradient of refractive index in rat lens have here been fitted by a continuous function and combined with the dioptric measurements of Hughes (1979a) to permit the derivation of an analytic, gradient index model lens and eye. The computed models are confirmed by comparison with optical measurements on the crystalline lens and with previous measurements on the eye (Hughes, 1977a, 1979a; Hughes and Wässle, 1979). *The observed close agreement is obtained without first fitting the model parameters to the experimental optical data.* These results have been reported in preliminary form (Campbell and Hughes, 1978).

The aim of this work is to produce a complete, anatomically based model of the rat eye which can predict aberrations, give insight into the eye design, and ultimately deal with oblique imagery without recourse to relaxation procedures.

THEORETICAL BACKGROUND

Basis of the gradient index lens model

Philipson's (1969) protein concentration distributions for rat crystalline lenses may be converted to

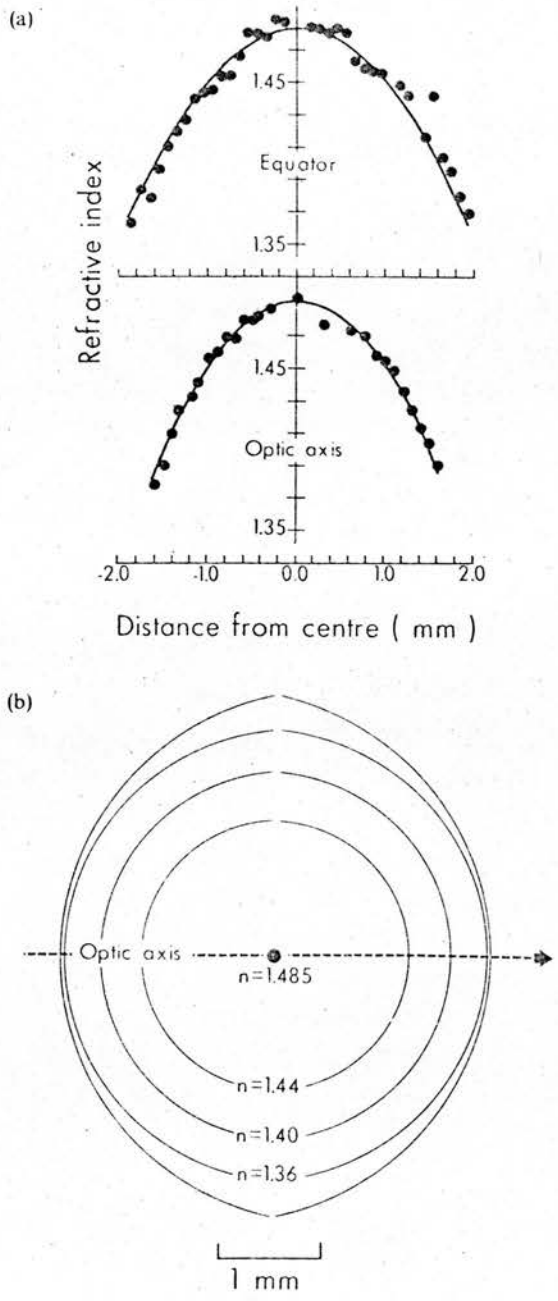

Fig. 1. (a) The points are data from Philipson's (1969) equatorial and axial profiles of the refractive index distribution for a 220 day old rat lens. The solid lines are the parabolic best fits for each axis which define the isoindicial circles of Fig. 1(b). These are off-centred from the lens centre by small amounts but, for calculation, the approximation was made that they are centred at the lens centre.

refractive index distributions by means of the Gladstone-Dale formula (Baer and Joseph, 1954). $n = 1.333 + \Delta n$ where Δn is the increase in refractive index above that of water. The consequent refractive index distribution for the equatorial and optic axes of a 220 day rat is shown in Fig. 1.

Philipson states that "lines connecting points with identical protein concentration form a more circular figure than the outer limit of the lens", Fig. 1b. For computation, the refractive index was therefore taken to depend on the radial distance, r, from the lens centre so that the true isoindicial surfaces are approximated by spheres:

$$n(r) = A - \frac{r^2}{B} \tag{1}$$

The constants $A = 1.4855$ and $B = 28.95$ were fitted to all but the most extreme points on each axis. A was varied between the limits 1.485 and 1.50 as indicated by Abbé refractometer readings (Philipson, 1969; Hughes, 1979a) and B was varied independently by $\pm 12\%$ based on systematic errors (Philipson, 1969). The actual distribution will lie well within these limits as the variations of A and B due to systematic error will be dependent.

The distribution, equation (1), was used in two forms. Model 1 assumes that the refractive index varies with the distance from the lens centre up to the surface of the lens so that the lens surface is not isoindicial. The value of refractive index near the equatorial poles is not allowed to drop below that of vitreous, 1.337. Model 2 assumes that the refractive index varies as the distance from the lens centre up to a value corresponding to the position of the poles on the optic axis. For radii greater than this the refractive index is constant at a value corresponding to the value at the poles.

$$n(r) = A - \frac{r^2}{B}, \; r < Z_{max} \tag{2}$$

$$n(r) = n(Z_{max}), \; r \geq Z_{max} \tag{3}$$

where Z_{max} is half the length of the optic axis. The lens surface is then isoindicial. The layer of constant index is limited by an inner spherical surface and the outer lens surface. The two models are very similar within the main body of the lens.

The capsule is a thin layer of uniform refractive index enclosing the lens. In model 1, it is ignored because its refracting power will be negligible. In model 2, the surface of the lens (corresponding to the capsule) has a constant index. Both models are expected to be good approximations to the real crystalline lens. The lens surfaces are treated as spherical caps of 2.34 mm radius and equatorial diameter of 4.23 mm (Hughes, 1979a).

Ray tracing through the gradient index lens model

Incident rays refract at the lens surface according to Snell's law. The ray equation,

$$\frac{d}{dS}\left[n \frac{d\vec{R}}{dS} \right] = \nabla n \tag{4}$$

then describes the continuous path of a ray through the lens. S is the path length of the light ray, dS is a differential increment of the path. $\vec{R}$ is the position of the ray relative to the origin (at the lens centre) $d\vec{R}/dS$ represents a tangent to the light ray at any point on its path and ∇n is the gradient of refractive index.

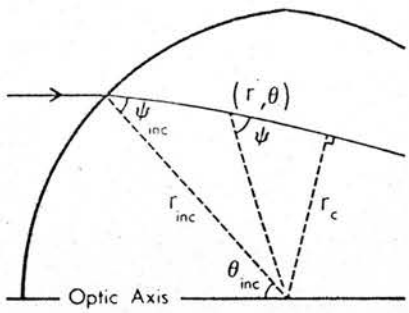

Fig. 2. Path of a ray through the lens model. The ray is confined to one plane. A constant of motion along the ray path is $c_2 = rn(r)\sin\psi$, calculated from the initial ray position after surface refraction. r_c is the minimum radial distance of the ray from the lens centre.

The solution of the ray path for a spherical distribution of refractive index, $n(r)$, has been discussed by Marchand (1973) and Born and Wolf (1975). The gradient of refractive index, ∇n, is nonzero only in the radial direction. This means that a ray travelling through the lens will remain in the plane defined by the initial ray direction (after surface refraction) and the direction of the position vector at the point of incidence. A second constant of motion, c_2, can then be derived.

$$c_2 = r\,n(r)\sin\psi \tag{5}$$

where r is the distance of the ray from the lens centre, $n(r)$ is the refractive index at this position and ψ is the angle between the ray direction and the position vector, Fig. 2. c_2 can be calculated from the initial ray position and direction after surface refraction. The ray path is then defined by expressing the angular coordinate at any point, θ, as a function of r. The exit position of the ray from the lens $(r_{\text{final}}, \theta_{\text{final}})$ is found by solving

$$\theta_{\text{final}} = \theta_{\text{initial}} + \Delta\theta \tag{6}$$

where

$$\Delta\theta = \pm c_2 \int_{r_{\text{initial}}}^{r_c} [r(r^2n^2(r) - c_2^2)^{1/2}]^{-1}\,\mathrm{d}r \mp c_2 \times \int_{r_c}^{r_{\text{final}}} [r(r^2n^2(r) - c_2^2)^{1/2}]^{-1}\,\mathrm{d}r \tag{7}$$

and

$$r_c n(r_c) = c_2 \tag{8}$$

simultaneously with the equation of the lens surface. The angle of incidence of the ray on the second surface of the lens is evaluated from equation (5). The exit angle of the ray is calculated using Snell's law at the posterior lens surface.

The fit of $n(r)$ to Philipson's data shows $n^2(r)$ to be a function of the second and fourth powers of r. The integral, equation (7) cannot be solved analytically and was evaluated by a numerical integration formula of the Gaussian type. (Abramowitz and Segun, 1970, p. 889). The solution of the ray equation is used in regions of variable refractive index and Snell's law is applied at the boundaries of the constant refractive index regions. This analysis has been incorporated in a computer program which generates the exit rays for rays incident in the meridional (or optic axis) plane.

Aberrations

Here we only consider monochromatic aberrations of a near axial image point; these are spherical aberration and coma which may be described in terms of ray or of wavefront aberrations. Ray aberration is the separation of the paraxial focal point from the intersection of a given ray with the paraxial focal plane, i.e. the distance l in Fig. 3, and is related to wavefront aberration. The formation of a perfect image requires the wavefront leaving the exit pupil plane to be a sphere centered at the paraxial image point. Wavefront aberration is the displacement of a given wavefront from this ideal reference sphere, W in Fig. 3. A system is said to be diffraction limited when its wavefront aberration is the displacement of a given wavefront from this ideal reference sphere, W in Fig. 3. A ration is less than a few wavelengths.

Spherical aberration. For an axial object point in a rotationally symmetric system, the ray aberration is the lateral spherical aberration.

$$l(\rho) = c_1\rho^3 + c_2\rho^5 \ldots \tag{9}$$

where c_1 and c_2 are the 3rd and 5th order spherical aberration coefficients, and ρ is the distance in the reference plane of the ray from the optic axis. The longitudinal spherical aberration is the distance between the paraxial image point and the crossing of the optic axis by the exiting ray, (δL).

From geometric considerations, Fig. 3.

$$\frac{\delta L(\rho)}{L + \delta L(\rho)} = \frac{l(\rho)}{\rho} \tag{10}$$

where $L + \delta L(\rho)$ is the distance along the optic axis between the reference plane and the crossing of the optic axis by the exiting ray. The magnitude of spherical aberration does not depend on the position of the reference plane, but the distribution among different orders does. For this analysis of spherical aberration, the back vertex plane of the lens was chosen as the reference plane, so that $L + \delta L(\rho) = \mathrm{BVD}(\rho_t)$ where BVD is the back vertex distance. Then

$$\frac{1}{\mathrm{BVD}(\rho_t)} = \frac{1}{\mathrm{BVD}(0)}[1 - c_1\rho_t^2 - c_2\rho_t^4 \ldots] \tag{11}$$

A plot of 1/BVD vs ρ_t^2 permits the third order and fifth order spherical aberration coefficients to be fitted.

Coma. As an object moves away from the optic axis, the variation in magnification factors in different regions of the lens causes an aberration known as coma. Coma is undesirable because it introduces assymetries into the image. Howland and Howland (1977) suggest that coma may not be negligible for man.

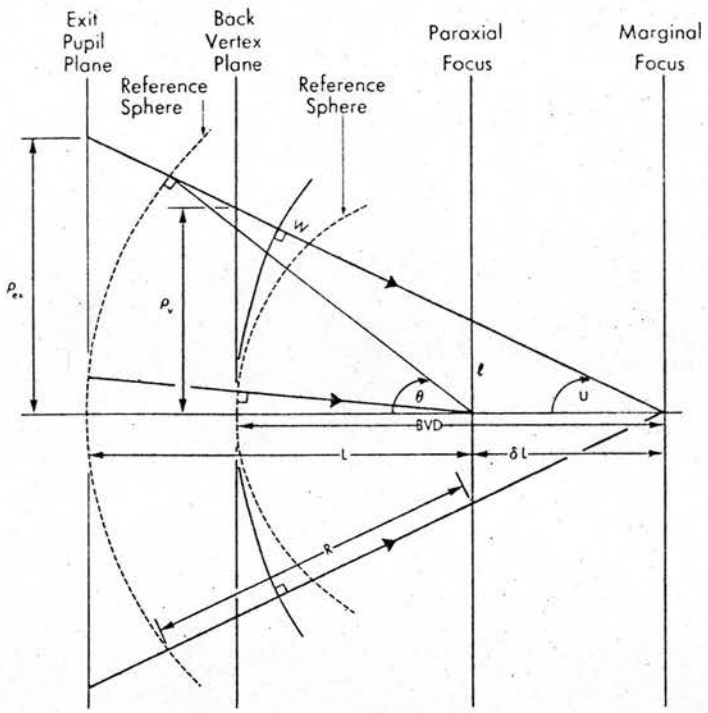

Fig. 3. l is the transverse ray aberration and W the wavefront aberration due to spherical aberration. δL represents longitudinal spherical aberration. For the analysis of spherical aberration, W is measured at the lens back vertex plane for each height of exit, ρ_v of a ray. The other variables are necessary to calculate the coma, corresponding to a saggital ray at position ρ_{ex} in the exit pupil, present in a point image slightly off-axis. Fig. 10 and equations 12–14.

Linear coma varies as the first power of the image height and produces a comet-like shape. For rays exiting from the sagittal exit pupil cross-section at a distance ρ_{ex} from the optic axis, the ratio of the transverse coma ray aberration $\Delta\eta$ can be expanded as an expression in even powers of ρ_{ex}:

$$\frac{\Delta\eta}{\eta} = -\frac{R}{n}\sum_i d_i\rho_{ex}^{2i} \qquad (12)$$

where n is the refractive index of image space, R is the distance from the exit pupil plane to the paraxial focal plane measured along the ray, and d_i are the linear coma coefficients.

Coma appears only for off-axis object points but its value can be calculated from axial measurements. For incident rays parallel to the optic axis,

$$Y(\rho_{ex}) = d_0[B(\rho_{ex})] + \sum d_i\rho_{ex}^{2i} \qquad (13)$$

where

$$Y(\rho_{ex}) = \frac{n\,[\cos u]}{L\,[\cos\theta]},$$

$$B(\rho_{ex}) = \frac{n[\cos u][f'(\rho_{ex})]}{[\cos\theta][L + \delta L(\rho_{ex})]} \qquad (14)$$

u, θ are angles defined in Fig. 3; $f'(\rho_{ex})$ is the distance measured along the ray from its intersection with the principal plane to its crossing of the optic axis; $[L + \delta L(\rho_{ex})]$ is the distance from the exit pupil plane to the crossing of the ray with the optic axis, measured along the optic axis; and L is the distance from the exit pupil plane to the paraxial image plane. This expression is valid over a large aperture and is related to the optical sine condition (Conrady, 1957). The MLAB program (Knott, 1970) is used to fit experimental and ray trace values of $Y(\rho_{ex})$ to the form on the right hand side to give values of d_0 and the linear coma coefficients, d_i. d_0 is the inverse of the paraxial posterior focal length, $(1/f'[0])$.

Unlike ray spherical aberration, ray coma in the paraxial focal plane of a system with spherical aberration depends on the choice of reference plane through the term $(L/[L + \delta L])$ (Welford, 1974). The reference plane is taken as the exit pupil plane estimated from Hughes' schematic eye for a 4 mm dia. aperture.

METHODS

DA rats of 120–140 days of age were anaesthetized by intraperitoneal injection of 1–2 cc of a 25% urethane solution. The enucleated eye was opened at the corneoscleral junction. The posterior surface of the crystalline lens was immersed in normal saline and inspected at ×25. The lens was then dissected free leaving some ciliary and zonule fibres intact for handling. The lenses chosen for use in this study were those with no obvious internal or surface opacities, little or no adherent iris after dissection and few secondary suture lines. Lenses were supported by a moulded cup after immersion in normal saline in a

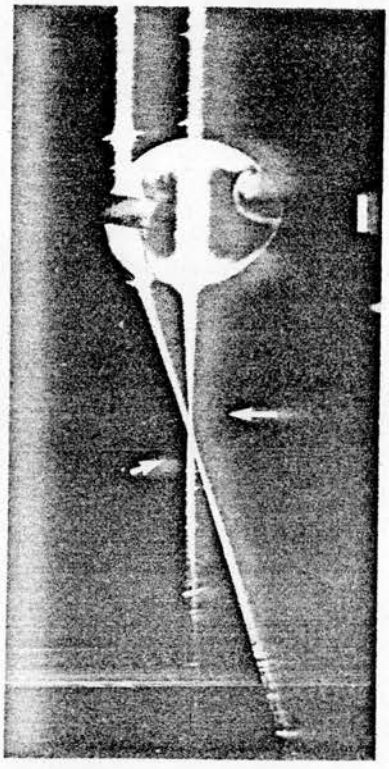

Plate 1. Axially and marginally incident laser beams are focused by a rat crystalline lens immersed in saline. The long arrow indicates the paraxial focus. The peripheral beam self focus is shown by the short arrow. The intersection of the two beams occurs behind the paraxial focus because of spherical aberration. Bar represents 1 mm.

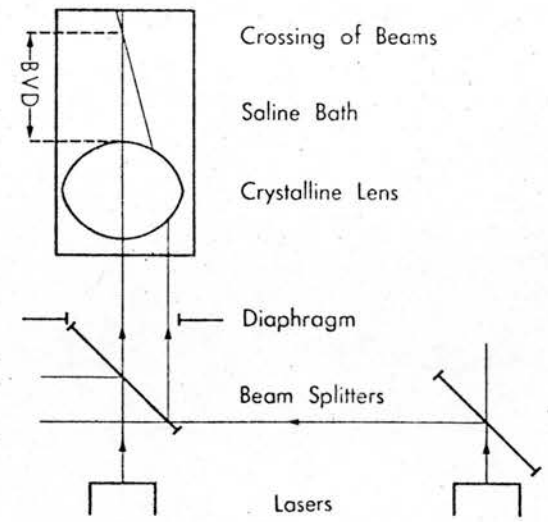

Fig. 4. Apparatus for measuring the back vertex distance (BVD) as a function of the height of the incident laser beam on the front of a crystalline lens. The crystalline lens and the beams in the saline bath were photographed from above.

bath with optically flat walls. A little fluorescein was added to the saline. The bath formed part of an optical bench system.

One He–Ne laser, with a wavelength of 630 nm, was fixed so that its beam traversed the centre of a beam splitter cube, Fig. 4. The crystalline lens was aligned so that this fixed beam was coincident with the optic axis. The beam from a moveable He–Ne laser was directed through two beam splitter cubes so that this second beam emerged parallel to the first. The separation of the beams was varied by scanning the beam of the mobile laser across the first beam splitter cube. The two 0.3 mm dia. laser beams passed through a 5 mm iris diaphragm to eliminate spurious reflections.

A camera was focused from above on the crossing of the beams leaving the crystalline lens. The stationary beam remained coincident with the optic axis as the mobile beam traversed the anterior surface of the lens at progressively larger separations. The self-focus of the fixed beam alone and the crossing of the two beams at each separation were photographed. For some series of pictures, the incremental separation of the beams was approx. 0.08 mm, while for others it was approx. 0.15 mm. The moveable laser beam was scanned across the complete horizontal diameter of the lens. A scale placed in the saline bath at the height of the laser beams was also photographed. Kodak S0410 and S0115 ESTAR-AH based films with extended sensitivity in the red region of the spectrum were employed. The exposure times required were between 4 and 30 sec. The film was developed in Kodak developer HC110, Dilution F for approx. 8 min. The absolute magnification on the negatives was 1.9.

The time from dissection until the end of the experiment was up to 4 hr. The condition of the lens at the end of the experiment was rechecked under $\times 25$ magnification. The results for any lens with defects were discarded. In order to check the influence of prolonged immersion on the optics, a lens was placed in the bath within 5 min of dissection and photographic exposures of two laser beams incident on the lens at a fixed separation were taken at times up to 5 hr after dissection.

Measurements of the developed films were made on the screen of a Nikon Profile Projector Model 6C fitted with a $\times 20$ lens. For a beam incident near the periphery of the crystalline lens the paths of the centre and edges of the beam could be resolved. Measurements of a beam photographed at different exposures were treated as independent. Between 40 and 100 sample points were obtained across the lens diameter dependent on the increment chosen.

THE CRYSTALLINE LENS

Computed results

Rays parallel to the optic axis were traced through the two computed lens models incrementing from the optic axis in steps of 2.5×10^{-2} mm up to the equatorial radius of the lens. The displacement of a ray from the optic axis is plotted in Fig. 5 against the separation of the point at which the ray crosses the optic axis from the back vertex of the lens (back vertex distance or BVD). The two models produce coincident results close to the optic axis but diverge significantly at some 1.25 mm from the optic axis. The central curves of Fig. 5 represent the values generated by the distribution fitted to Philipson's data. The shaded region corresponds to values of Philipson's protein distributions within the estimated extreme limits. The paraxial back vertex distance for the models is 3.58 mm ranging from 3.01 mm and 3.90 mm. The intersection of the traced ray with the optic axis moves away from the lens for more peripheral rays. This is defined here as negative or undercorrected spherical aberration (Hughes, 1979a).

Experimental results

Figure 6 plots displacement of the incident beam from the optic axis against the separation of the intersection of the exit beam with the axial beam from the back vertices of 3 selected lenses (back vertex distance or BVD). The displacement of the intersection of the exit beams from the axial beam focus was small within 0.75 mm of the optic axis, but, it becomes very large close to the lens periphery in agreement with the predictions of the gradient index model.

Comparison of experimental results and computed ray traces

Absorption of water and chromatic aberration were only small sources of discrepancy between the experimental results and the computed ray trace. The back vertex power of a lens immersed in saline for several hours was observed to change by only 3%. The use of

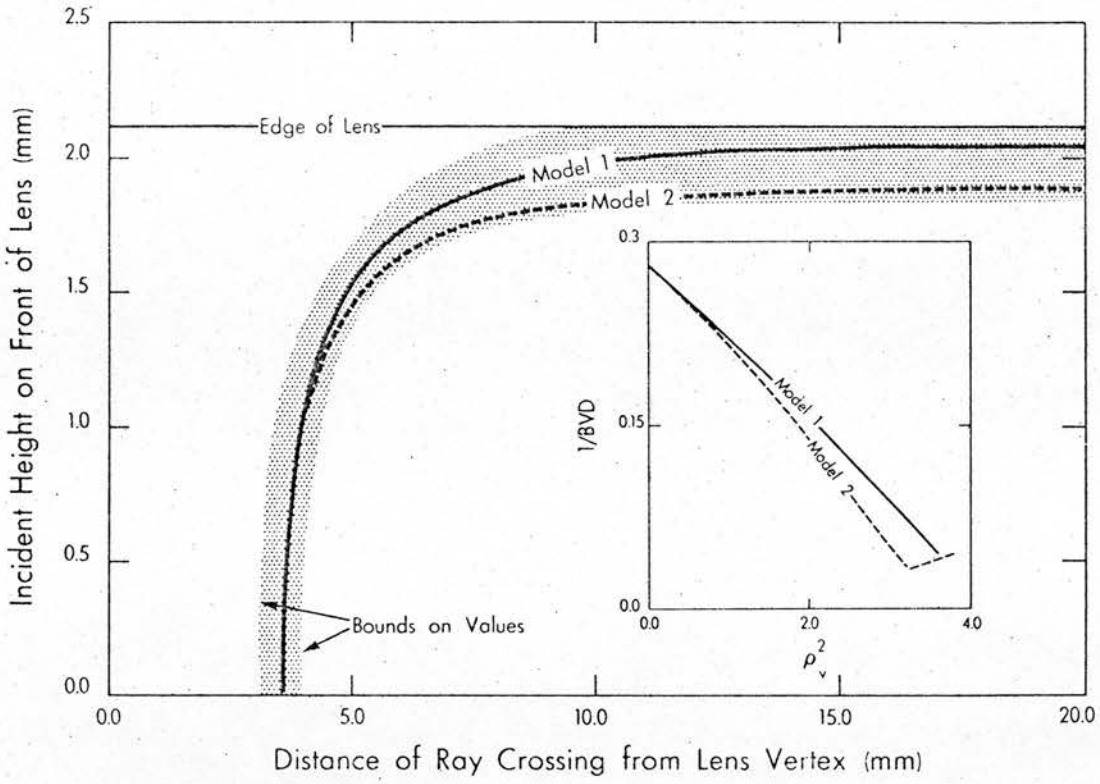

Fig. 5. Theoretical Results. The results of computed ray traces through the lens models. The height of an incident ray from the optic axis is plotted against the distance from the back vertex of the lens (BVD) to the optic axis crossing by the corresponding exiting ray. The solid curve represents model 1 (for which the lens surface is not isoindicial) and the broken curve, model 2 (for which the lens surface is isoindicial). The shaded area represents ray traces corresponding to the range of possible fits to Philipson's data. The extreme bounding values of the ray traces are indicated by arrows. These plots demonstrate the negative spherical aberration of the lens models. The inset shows a plot of the inverse of the back vertex distance, 1/BVD, against the square of the ray height at the back vertex plane ρ^2. From this plot and equation 11, the spherical aberration coefficients can be derived. The near linearity of this plot shows that the spherical aberration is primarily 3rd order.

a He-Ne laser light instead of a yellow-green source increased the measured lens focal length by about 0.5%. Philipson's (1969) data from adult rats of various ages shows little variation and this is exceeded by the experimental uncertainty. It is thus justifiable to compare a theoretical analysis based on his detailed distribution for 220 day rats with experimental observations on eyes from 120–140 day old animals.

Spherical aberration. The gradient index model and the experimental results can be compared by fitting 1/BVD vs ρ_v^2 (equation 11) and calculating the third and fifth order spherical aberration coefficients relative to the back vertex plane of the lens.

For a linear regression analysis the fit in third and fifth order coefficients changes slightly as the maximum incident height, or aperture, is varied. The fitted paraxial back vertex distance and aberration coefficients for various apertures are given in Tables 1F for the experimental results and 1E and 1G for the ray trace results respectively.

The fifth order spherical aberration term is small in the gradient index model as seen from the near linearity of the plot in the inset of Fig. 5 and the comparison of the total ray aberration with that from third order in Table 1G. Fifth order aberration was not significant for 2 of the 3 experimental rats. The experimental and model fits were thus compared only to third order. The correlation of the model fit is better than 99% and is 87%, 90% and 95% respectively for the three experimental lenses.

Given that the spherical aberration is primarily third order, the positions of the discs of least confusion can be estimated. According to the ray approximation (Welford, 1974) the disc of least confusion falls 3/4 of the distance from the intersection of the paraxial ray to the intersection of the marginal ray with the optic axis. This position is compared to Hughes' 1979a experimental measurement with a 2 mm dia aperture, Tables 1C and 1D.

The experimental back vertex distances, Fig. 6, and position of the disc of least confusion, Table 1, are within the range predicted by the ray trace. The spherical aberration coefficients for the experiments and ray traces are also in reasonable agreement.

Coma. $Y(\rho_{ex})$ (equation 13) was very scattered for the experimental results and was fitted to the second order linear coma term in an order of magnitude esti-

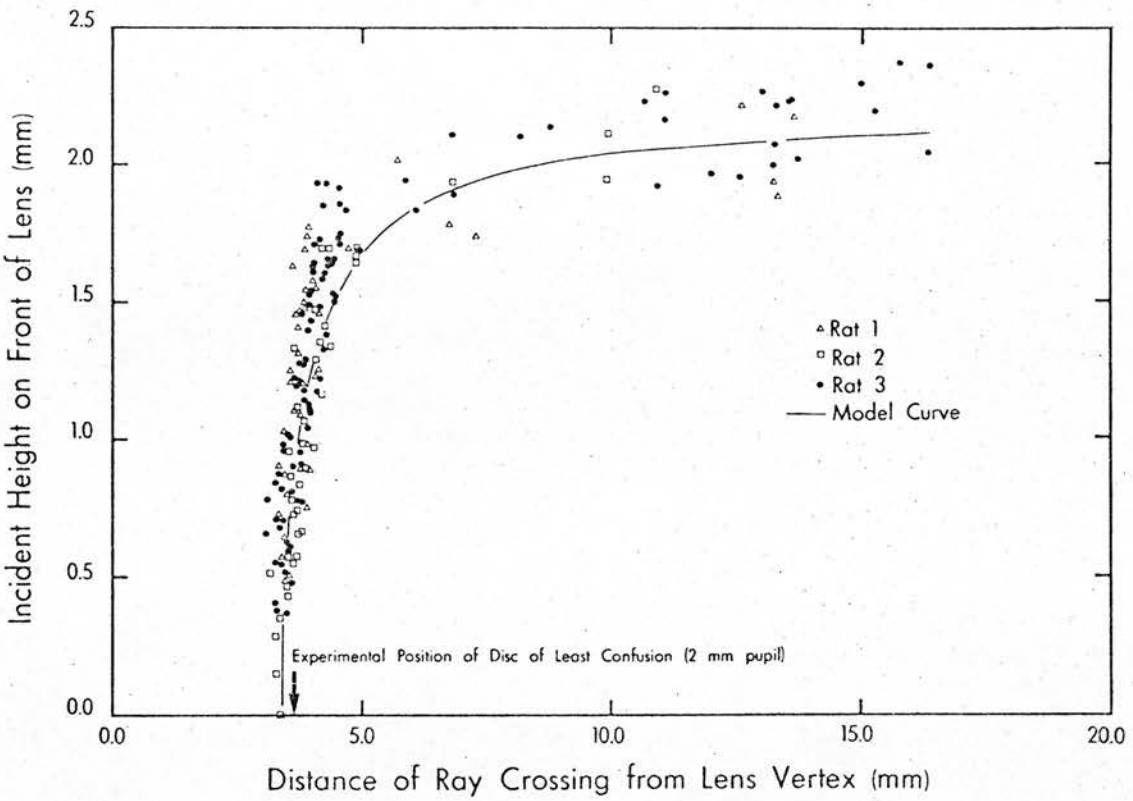

Fig. 6. Experimental Results. The measured incident ray separation is plotted against the distance of intersection of the two rays from the back vertex of the crystalline lens. One ray is incident along the optic axis while the height of the other ray is variable. (See Fig. 4). Results are shown for crystalline lenses of three different rats; the solid curve from Fig. 7 is shown for comparison. The position of the disc of least confusion is from Hughes (1979a).

mate, Table 1F. This is compared to a fit of the gradient index models with maximum aperture to the same second order linear coma term, Table 1F. The expansion of the model coma in first and second order is given in Table 2E. All three experimental lenses show the same order of magnitude value of linear coma and focal length as the lens models.

The gradient index lens models predict all the measured and calculated optical properties within the accuracy of Philipson's measurements and within experimental uncertainty. The agreement of the model with experiment supports Philipson's data and our treatment of it.

Reestimate of the parabolic constants of the gradient index distribution

From the experimental results it is obvious that closer bounds can be placed on the range of Philipson's measurements. The paraxial back vertex distance is not expected to be as small as 3.01 mm or as large as 3.90 mm. After correcting the experimental back vertex measurement to compensate for osmotic absorption and chromatic aberration, there exists a family of model curves which will give a disc of least confusion for a 2 mm dia aperture at the experimentally measured position and a paraxial focal length within the range measured. For example, for model 1, a central index of 1.4855 and a parabolic constant of 26.6, or 1.49 and 27.2 or 1.50 and 28.9 fit the results. The separation of the most likely bounding curves based on optical measurements and Philipson's data is then reduced, Fig. 7. The curves shown represent the following range in the parabolic constants of equation (1): for $A = 1.485$ $B = 26.0$–27.0, for $A = 1.49$ $B = 26.8$–27.8, for $A = 1.50$ $B = 28.4$–29.4. The reversal of the curve corresponding to model 2 occurs in Figs 5 (inset) and 7 in the equatorial region of the lens when the spherical aberration of the region of constant index overbalances that of the gradient index region.

The distribution most likely to represent the crystalline lens accurately has a central index of 1.50 in accord with refractometer readings (Hughes, 1979a; Philipson, 1969) and a parabolic constant of 28.9. Its optical properties are displayed in Fig. 7 and Tables 1D, E and G for models 1 and 2. The third order spherical aberration coefficient is little different from that of the original distribution but the paraxial back vertex distance is shorter.

The compressed range of index distributions will be used in a discussion of the crystalline lens and whole eye properties. These models accurately approximate the rat lens apart from some uncertainty in the equatorial regions.

Table 1. Crystalline lens data

Experimental Results

(A) Physical parameters

	Mean	Average eye SEM
Surface radii (mm)	*2.34	0.03
Equatorial diameter (mm)	*4.23	0.077
Lens thickness (mm)	3.82	0.06
	*3.71	0.05
Aqueous and vitreous refractive index	*1.337	–

*From Hughes (1979a)

Fit to Philipson's (1969) Lens refractive index distribution:

$N(r) = A - r^2 B$

A = 1.4855 with extremes of 1.4855, 1.50

B = 28.95 ± 3.5

(C) Optical measurements

	Rat 1	Rat 2	Rat 3
Paraxial back vertex distance (BVD) (mm)	3.41	3.32	3.26
Corrected, averaged BVD		3.40 ± 0.07 mm	

	Mean (mm)	Average eye SEM (mm)
Distance of disc of least confusion from lens back Vertex (2 mm dia pupil) From Hughes (1979a)	3.64	0.045

Model Results

(B) Model parameters—all models

Anterior and posterior surface radii			2.340 mm
Lens thickness			3.710 mm
Lens equatorial radius			2.115 mm
Refractive indices			
Aqueous and vitreous			1.337
Schematic homogeneous lens	—total index		1.683
Core model lens	—lens cortex		1.390
	lens core		1.500
	core surface radius		0.958 mm
Gradient index lens	$N(r) = \alpha - r^2 \beta$		
Initial models A_1, A_2	α = 1.4855	bounds	1.4855, 1.50
	β = 28.95	bounds	25.5, 32.4
Refitted models B_1, B_2	α = 1.50	bounds	1.4855, 1.50
	β = 28.9	bounds	26.0, 29.4

(D) Paraxial results

	A_1, A_2	B_1, B_2
Paraxial back vertex distance (BVD) (mm)	3.578 (3.01, 3.90)	3.398 (3.27, 3.44)

	A_1	A_2	B_1	B_2
Distance of disc of least confusion from lens back vertex (2 mm dia pupil) (mm)	3.870	3.898	3.638	3.653

(E) Comparison of lens models—paraxial results

	Homogeneous model	Core model	Gradient index model, B	Bounds on B
Power (D)	247.6	244.0	255.2	253–261
Anterior surface power (D)	147.9	22.6	18.8	6.5–19.6
Posterior focal length (mm)	5.401	5.420	5.239	5.12–5.29
Paraxial back vertex distance (mm)	3.64	3.64	3.398	3.27–3.44
Principal and nodal point distance from lens centre (μm)	94	15	13	5–14

(F) Aberrations

Spherical aberration (Units mm)

Aperture radius	Rat 1 BVD_0	Rat 1 C_1	Rat 2 BVD_0	Rat 2 C_1	Rat 3 BVD_0	Rat 3 C_1
2.115	3.26	0.17	3.42	0.22	3.27	0.21
1.5	3.48	0.09	3.44	0.20	3.33	0.20
1.0	3.43	0.14	3.36	0.32	3.28	0.26

Coma

Rat	d_0	Posterior focal length, f' (mm)	d_2
1	0.192	5.2 ± 0.1	$0.3 \times 10^{-3} \pm 0.3 \times 10^{-3}$
2	0.183	5.5 ± 0.2	$-0.7 \times 10^{-3} \pm 0.9 \times 10^{-3}$
3	0.176	5.7 ± 0.1	$-0.4 \times 10^{-4} \pm 0.3 \times 10^{-3}$

(G) Aberrations—gradient index models

Spherical aberration (Units mm)

Model	Aperture radius	C_1	Bounds	Max l'	3rd order l'
A_1	2.115	0.23	0.19–0.25	1.81	1.86
A_2	2.115	0.22	0.16–0.26	1.28	1.56
B_1	2.115	0.21	0.21–0.26	1.51	1.49
B_2	2.115	0.24		1.40	1.59
A_1	1.5	0.21	0.16–0.25	0.30	0.29
A_2	1.5	0.23	0.18–0.27	0.34	0.33
B_1	1.5	0.19	0.19–0.27	0.25	0.25
B_2	1.5	0.22		0.30	0.29
A_1	1.0	0.20	0.15–0.25	0.068	0.068
A_2	1.0	0.22	0.17–0.26	0.074	0.074
B_1	1.0	0.19	0.18–0.26	0.058	0.058
B_2	1.0	0.20		0.064	0.064

Coma for maximum aperture

Model	d_0	Posterior focal length, f' (mm)	d_2
A_1	0.184	5.43	-0.816×10^{-3}
A_2	0.184	5.43	-0.881×10^{-3}
B_1	0.1908	5.24	-0.734×10^{-3}
B_2	0.1911	5.23	-0.107×10^{-2}

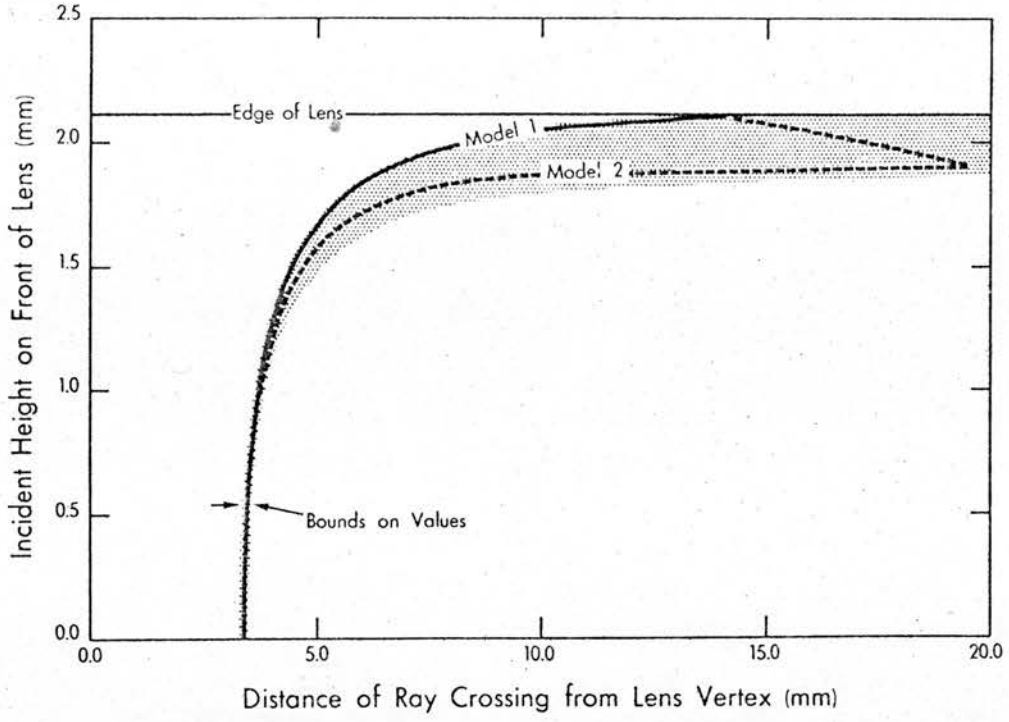

Fig. 7. Theoretical Results. The model refractive index distributions have been reestimated within a smaller range after comparison of the theoretical predictions with experimentally measured optical properties of the crystalline lens. The plot is analogous to that of Fig. 5.

A comparison of the gradient index lens model with the homogeneous and core models of Hughes (1979a)

Hughes (1979a) has derived two paraxial rat schematic eyes; one employs a homogeneous lens and the other a two-shell core lens which were fitted by a relaxation procedure to a finite pupil BVD measurement. The above gradient index model of the lens differs from that of Hughes (1979a), and from other schematic eyes, in that it was initially based on anatomical and refractive index measurements alone. The model was not fitted to measured focal properties which are employed only to confirm the model and to reduce the original bounds on Philipson's values.

The paraxial power of the core model is less than that of the homogeneous lens, Table 1E. This is caused by the shift of the principal planes towards the core lens centre. The principal planes move still closer to the lens centre in the gradient index model so that the lens power could be expected to decrease relative to the core lens by 0.1 D. However the power of the gradient index model remains greater because it predicts the true paraxial back vertex distance rather than that for a finite aperture.

The homogeneous and core model lenses are valid within the paraxial region alone so that the back vertex distance should have been fitted to the measured *paraxial* back vertex distance not to a disc of least confusion for a finite pupil. For the rat lens the difference between a fit to a paraxial back vertex distance and to the disc of least confusion used was 11 D. This accounts for most of the difference in power between the core lens model of Hughes (1979a) and this gradient index model.

The power of the lens in the homogeneous model is entirely attributed to the surfaces of the lens; the surface power of the core and gradient index models is lower. Because the surface curvatures in all models are identical, these differences in power arise from differences in the refractive indices at the lens surface. The centres of curvature of the lens surfaces are not concentric with the centre of the lens and draw the principal points away from the centre of the lens in proportion to their power (Helmholtz, 1909). Even if the correct back vertex power is employed the principle planes will be too far apart and the power overestimated when a homogeneous lens models a crystalline lens with a spherical refractive index gradient.

The similarity between the principal plane positions of the core and gradient index model lenses implies that a core model is valid for paraxial rays when it is fitted to the true paraxial back vertex distance. However, paraxial optics apply only at small pupil sizes in the rat because of the large spherical aberration.

A GRADIENT INDEX MODEL EYE

The whole eye model

A refractive index distribution with bounding values has thus been chosen from the range of Philipson's results as most probably representing the actual anatomy of the rat crystalline lens. Fig. 7. The two gradient index lens models based on this, with vari-

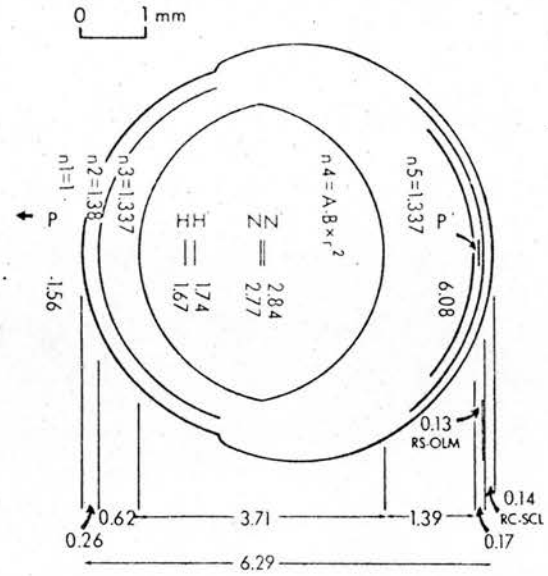

Fig. 8. The eye model drawn to scale and presenting the paraxial focal properties which are identical for models 1 and 2. Measurements are given in millimetres from the corneal vertex and between points indicated by arrows. The refractive indices of the various media are signified by the prefix n. The model resembles that of Hughes (1979a). Fig. 4, except that the lens has a gradient refractive index. The focal length is shorter and the paraxial refractive state is slightly myopic. RS-OLM—Retina surface to outer limiting membrane, RC-SCL—Retina/choroid interface to posterior scleral surface.

able surface refractive index and constant surface refractive index respectively, were then combined with the radii of curvature and relative positions of the ocular surfaces (Hughes, 1979a), Table 2A, to produce two model eyes, Fig. 8.

Rays incident parallel to the optic axis were traced in steps of 2.5×10^{-2} mm up to the measured corneal height. Snell's law was applied at the corneal surfaces and the lens treated as previously.

The displacement of the incident ray from the optic axis at the point of incidence on the cornea is plotted vs the distance at which the ray crosses the optic axis from the back vertex of the lens (BVD), Fig. 9. The curves are the computed results for the most likely index distribution and the shaded region represents the bounding values of the whole eye ray traces generated by the range of lens refractive index profiles. The two schematic eye models produce coincident ray traces close to the optic axis, Fig. 9. The reversal of the curve for model 2 in the periphery occurs when the aberration of the region of constant index in the lens and of the cornea overbalances that of the gradient index region of the lens.

Paraxial properties

Paraxial values are the limits of quantities calculated for a parallel incident ray as it approaches the optic axis. They are displayed in Table 2B and compared with Hughes (1979a) core lens schematic eye. The homogeneous model will be ignored as totally inadequate. The chosen parabolic refractive index profile was that with $A = 1.50$, $B = 28.9$ in equations (1–3). The bounding paraxial values correspond to the two limits placed on the refractive index profile. ($A = 1.50$, $B = 29.4$ and $A = 1.4855$, $B = 26.0$). The two limiting refractive index profiles will give rise to the outer limits on whole eye power and on focal lengths.

The focal plane of the gradient index model is 0.1 mm closer to the cornea than that of the core lens model (Hughes, 1979a). The focal length of this model is shorter and the power of the eye is greater than that of the core model eye because its gradient lens has higher power. The principal and nodal points of the eye are closer together because of the gradient of refractive index in the lens. The principal points shift towards, and the nodal points away from the retina.

Spherical aberration

The whole eye ray traces, Fig. 9, display substantial negative spherical aberration in agreement with Hughes (1977a). The aberration coefficients can be calculated by fitting 1/BVD vs p_v^2 where p_v is the height of the beam in the back vertex plane. The fit of spherical aberration was performed for various apertures, Table 2E. The fifth order coefficient was small for most apertures (Fig. 9 and Table 2E) and only the third order was considered.

The given aberration coefficients make possible a comparison of the wavelength aberration of the lens and of the whole eye (Welford, 1974). At maximum aperture, the wavefront lags behind the reference sphere by about 800 wavelengths for the lens whereas for the whole eye model it lags by about 100 wavelengths. The ray aberration, l, also decreases by a factor of 1/8th between the crystalline lens and the whole eye, Tables 1G, 2E.

The cornea has positive spherical aberration (Hughes, 1979a) which thus compensates to a large extent, but not totally, for the negative spherical aberration of the lens. This model shows the aberration increasing progressively with beam displacement from the optic axis rather than abruptly beginning in the peripheral pupil outside the lens core (Hughes, 1979a).

The negative spherical aberration of the whole eye model is of similar magnitude to that measured by Hughes (1977a). A parallel beam incident near the margin of a fully dilated, 4 mm dia pupil required 6–8 D more power for optometric refraction than a parallel beam confined to the centre of the pupil (Tables 2D and 2E). The difference in power of the eye between an axial ray and any ray in the periphery may be calculated for the eye models, Table 2I. Because there is some question of the exact position and width of the peripheral beam in the experimental measurement it should be compared to the values calculated for beams incident at dia of 3–4 mm. The power difference for a ray for the two models was 5.4 D and 7.5 D respectively for a ray incident at

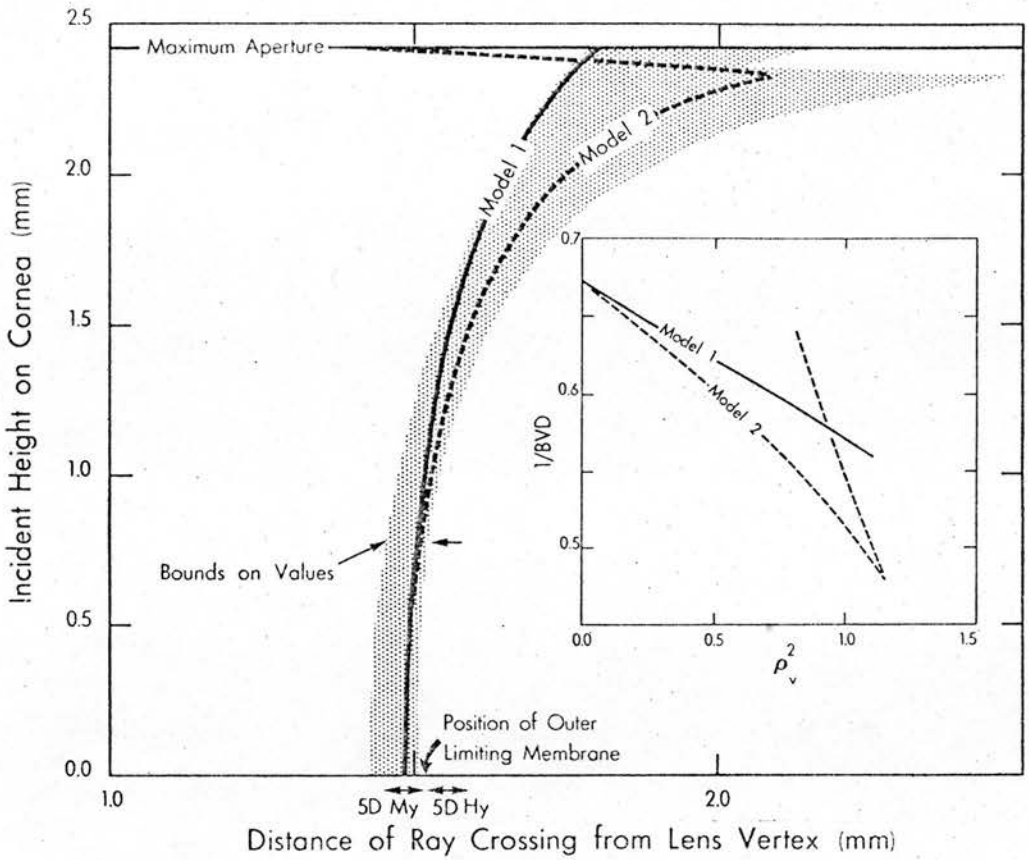

Fig. 9. The results of the computed ray trace through the complete eye for models 1 and 2. The distance of the ray incident on the cornea from the optic axis is plotted against the distance from the back vertex of the lens to the optic axis crossing by the exiting ray (BVD). The shaded area shows the region into which the models corresponding to the range of refractive indices fall (see Fig. 7). Distances corresponding to 5 dioptres of myopia and 5 dioptres of hypermetropia are shown and the arrows indicate the bounding ray trace values. The inset plots the inverse of the back vertex distance, 1/BVD, against the square of the ray height at the back vertex plane. The relationship is close to linear, as for the lens, and demonstrates the predominance of 3rd order spherical aberration. The position of the outer limiting membrane is from Hughes (1979a).

1.5 mm and 11.0 D and 17.4 D at 2 mm, Table 2I. The model predicts the measured magnitude of spherical aberration if the experimental beam fell within the 4 mm pupil.

Coma

Using equations (13, 14) and the fitting program, MLAB, $Y(\rho_{ex})$ was fitted to ρ_{ex}^2 for the whole eye models. The first coefficient d_0 corresponds to the inverse of the posterior paraxial focal length and the fitted value agrees with that already derived in Table 2B. The coma in an image expressed as the ratio of the transverse ray aberration to the image height can be related to $Y(\rho_{ex}) - d_0[B(\rho_{ex})]$ via equations (12) and (13). This is plotted in Fig. 10 for the lens alone and for the whole eye for both of the gradient index models. The plots have been normalized so that the exit pupil radius ranges from zero to one. The coefficients of linear coma to second order in ρ_{ex}^2 are given in Table 2E but some higher order dependence remains at large pupils, Fig. 10.

The amount of coma increases with increasing pupil radius and only decreases in the second lens model when coma due to the lens surface exceeds that due to the gradient of refractive index. Except for rays through the extreme of the exit pupil, the coma due to the lens alone is of the same sign as the whole eye but is much larger in magnitude. The coma due to the cornea largely but not completely balances that due to the lens.

The calculated linear coma for incident light filling only one half the maximum exit pupil corresponds to a change in the sagittal magnification factor of between 1/75th and 1/100th across the pupil for the lens alone and of 1/300th for the whole eye. For light nearly filling the maximum exit pupil, the saggital magnification factor will change by 1/8th across the image for the lens alone and by 1/70th for the whole eye. For small, and possibly large, pupils the linear coma for the whole eye would be below the resolving power of the retina.

The refractive state of the whole eye

A knowledge of spherical aberration in the whole eye enables the focal plane position to be calculated for each pupil diameter. There are two possible cri-

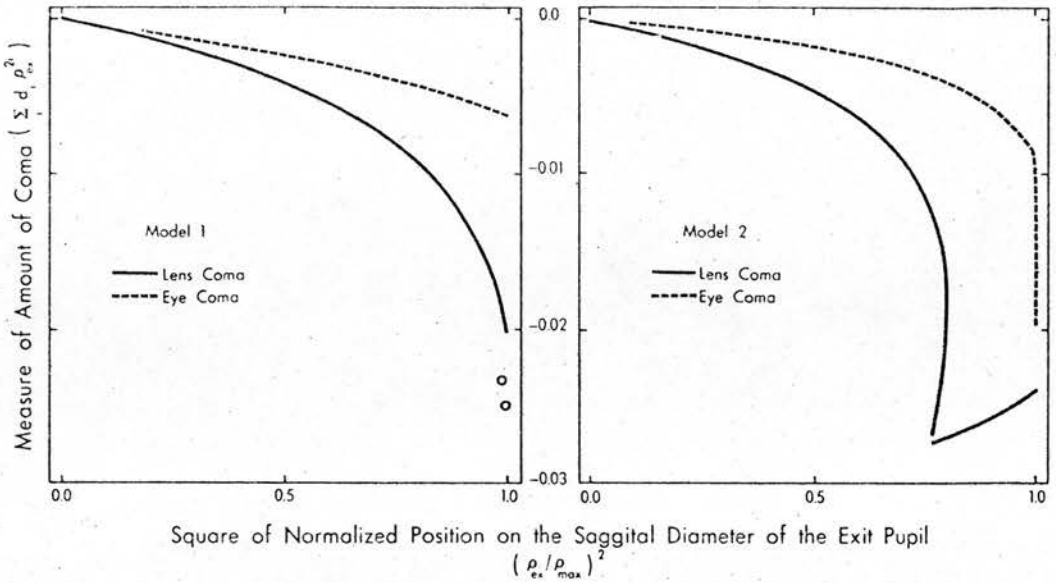

Fig. 10. Coma for the lens and the whole eye models. A value for $(\rho_{ex}/\rho_{max})^2$ of 1.0 is equivalent to a ray entering the margin of the maximum entrance pupil. The ordinate represents a negative multiple of the change in magnification factor (equation 12) and a corresponding increase in coma. The magnification factor increases rapidly as more marginal rays are considered and the image displays more coma. The coma of the eye is less than that of the lens for both models so that the cornea must partly compensate for lens coma.

teria for the location of the plane of best focus (Welford, 1974). In systems with no more than 1 wavelength of spherical aberration it is taken as the plane at which the central intensity of the point image is at a maximum. For third order axial spherical aberration this plane occurs at one-half the distance between the paraxial ray crossing of the optic axis and the marginal ray crossing of the optic axis. In systems with more than 1 wavelength of aberration, the position of the disc of least confusion is the criterion for the plane of best focus. For third order aberration this is located (Welford, 1974) three-quarters of the distance between the paraxial ray crossing of the optic axis and the marginal ray crossing of the optic axis. One wavelength of spherical aberration is present in the model for a pupil of 1.9 mm dia; the extreme values are 1.75 mm and 2.05 mm. The estimated planes of best focus for different pupils are given in dioptres in Table 2E.

With one quarter wavelength of spherical aberration present, the image intensity distribution and the cut-off frequency approach that of a perfect diffraction limited system (Smith, 1966). From the model, the maximum pupil diameter allowed under these conditions is 1.35 mm with possible extremes of 1.25 mm to 1.45 mm. Experimental measurements (Hughes and Wässle, 1979) suggest poorer quality optics; the pupil diameter is 0.33 mm or less before the point spread function approaches that expected from diffraction alone, Table 2H. However, their results incorporate chromatic aberrations and scattering and were based on a double pass technique which might underestimate optical quality. Hughes and Wässle's (1979) results do display the loss of acuity with increasing pupil size which would be predicted by this model for pupils larger than 1.35 mm dia.

The variation of the refractive state of the rat eye with pupil size may be compared with the experimental measurements of Hughes (1977a) (Tables 2D and 2F). The refractive state, k in dioptres, is defined as,

$$k = \frac{n}{d - A_1H'} - \frac{n}{H'F'} \qquad (15)$$

where n is the refractive index of vitreous, $(d - A_1H')$ is the distance of the effective image shell—the outer limiting membrane—and $H'F'$ is the distance of the position of best focus from the second surface of unit magnification measured along the principal ray.

In a perfect optical system with no spherical aberration or coma, the surface of unit magnification would be spherical (Jenkins and White, 1951). The gradient index eye has a more general unit surface shape given in Fig. 11. The predicted refractive state is calculated as a function of pupil diameter, Table 2I. The calculation of the refractive state for marginal rays involved the introduction of a prismatic correction to equation (15).

The paraxial refraction of the two rat eye models above is -2.5 D with a range (from -1.1 D to -6.6 D) corresponding to the uncertainty in the lens model refractive index distributions. The individual variation between eyes may be greater (Hughes, 1979a). The eye model predicts that the refractive state of the eye will be myopic to emmetropic for paraxial rays and small finite pupils, Table 2I. The model predicts that the plane of best focus will shift

Table 2. Whole eye data

Parameters For All Models

(A) Based on Hughes (1979a) and combined with the lens models, Table 1

Cornea refractive index	1.38
Anterior corneal radius	2.965 mm
Posterior corneal radius	2.705 mm
Cornea base radius	2.82 mm
Posterior scleral curvature	3.23 mm
Positions of surfaces	
Anterior corneal surface	0.000 mm
Posterior corneal surface	0.260 mm
Anterior lens surface	0.881 mm
Posterior lens surface	4.591 mm
Retina surface	5.931 mm
Outer limiting membrane	6.111 mm
Posterior scleral surface	6.291 mm

Experimental Results

(C) From Hughes (1979a)

	Mean (mm)	SEM (mm)
Measured PND = PND + d + 0.03 mm	3.39	0.03
Corresponding paraxial retinal magnification mm/deg	0.0586	0.006

(D) From Hughes (1977a)

Paraxial refractive state (D)

Small pupil slit retinoscopy		*9.4
Direct ophthalmoscopy		*8.0
*Plane of refraction is postulated to be vitreal plane		
Neurophysiological refraction		0 ± 5
Optometric refraction	Surface nerve fibres	8.25
	Surface vessels	8.6
	Choroidal vessels	−2.1

Displacements in dioptres—gradient index model

Choroidal vessels from focal plane of the eye	−5.2
Retinal surface from focal plane of the eye	+6.9
Choroidal vessels to vitreal retinal surface	+12.2

(F) From Hughes (1977a)

Non-paraxial refractive state (D)

Retinoscopy		indeterminate
Optometric refraction		
2.0 mm pupil	Surface vessels	9.0
4.0 mm pupil marginal rays	Surface vessels	17.0
	Choroidal vessels	4.5
Neurophysiological refraction		6.0

(H) From Hughes and Wässle (1979)

Image quality

	Pupil diameter (mm)	Single pass angular period at cut-off (min arc)	Airy disc dia mm at paraxial focus
Rat 1:	0.33	12.5	1.2×10^{-2}
	1.0	14.0	1.3×10^{-2}
	2.5	19.3	1.9×10^{-2}
Rat 2:	0.33	13.0	1.3×10^{-2}
	1.0	15.0	1.4×10^{-2}
Rat 3:	0.33	13.9	1.3×10^{-2}
Rat 4:	3.0	36.0	3.5×10^{-2}

Model Results

(B) Comparison of eye models—paraxial results (mm from cornea)

	Core model	Gradient index model, B	Bounds on B
Paraxial back vertex distance	1.587	1.485	1.428–1.504
Anterior principal plane position	1.651	1.674	1.668–1.694
Posterior principal plane position	1.732	1.745	1.740–1.748
Anterior nodal point position	2.771	2.765	2.765–2.770
Posterior nodal point position	2.852	2.837	2.825–2.838
Posterior nodal point to retinal surface	3.159	3.274	3.273–3.286
Anterior focal length = −PND	−3.326	−3.239	−3.195, −3.257
Posterior focal length	4.446	4.331	4.271–4.354
Posterior focal plane position	6.178	6.076	6.020–6.095
Out of focus distance, d (mm)	+0.067	−0.035	−0.016, −0.092
Power (D)	300.7	308.7	307.0–313.0
Paraxial refractive state (D)	+4.6 ± 1.7	−2.5	−1.1, −6.6
Paraxial retinal magnification (mm/deg)	0.058		
*Emmetropic model value	*0.0569*	0.0571	0.0571–0.0574

(E) Non-paraxial results—gradient index model

				Spherical aberration (units mm)	
Model	Lens aperture radius	C_1	Bounds	Maximum 3rd order l	l
B_1	2.115	0.15	0.14, 0.31	0.178	0.175
B_2	2.115	0.22		0.310	0.163
B_1	2.0	0.15	0.14, 0.32	0.131	0.131
B_2	2.0	0.22		0.251	0.229
B_1	1.5	0.16	0.14, 0.32	0.039	0.039
B_2	1.5	0.21		0.055	0.055
B_1	1.0	0.16	0.15, 0.32	0.010	0.010
B_2	1.0	0.21		0.013	0.013
B_1	0.5	0.16	0.15, 0.33	0.001	0.001
B_2	0.5	0.21		0.001	0.001
B_1	0.25	0.16	0.15, 0.33	1×10^{-4}	1×10^{-4}
B_2	0.25	0.21		2×10^{-4}	2×10^{-4}

Coma (Taylor series expansion)

Model	d_0	Posterior focal length, f', mm	d_1	d_2
Lens B_1	0.1908	5.240	-0.13×10^{-2}	-0.13×10^{-3}
Eye B_1	0.2309	4.331	-0.61×10^{-3}	-0.11×10^{-4}
Lens B_2	0.1908	5.240	-0.12×10^{-2}	-0.14×10^{-3}
Eye B_2	0.2309	4.331	-0.42×10^{-3}	-0.36×10^{-4}

(G) Nodal point positions (mm from cornea)

Incident ray angle (rad)	Model 1 Anterior nodal point	Model 1 Posterior nodal point	Model 2 Anterior nodal point	Model 2 Posterior nodal point
Paraxial	2.765	2.837	2.765	2.837
0.1	2.767	2.838	2.767	2.838
0.2	2.765	2.836	2.765	2.837
0.5	2.765	2.834	2.765	2.837
0.75	2.766	2.831	2.764	2.838
1.0	2.767	2.827	2.763	2.839
1.31	2.770	2.819	2.761	2.841

Table 2. Whole eye data—continued.

Model Results

(I) Focal plane data

Entrance pupil dia (mm)	Airy disc width-perfect system (mm)	Model 1			Model 2		
		Disc of least confusion width (mm)	Refractive state (D)-plane of best focus	Refractive state (D)-marginal ray	Disc of least confusion width (mm)	Refractive state (D)-plane of best focus	Refractive state (D)-marginal ray
Paraxial	$\rightarrow\infty$	$\rightarrow 0$	−2.5	−2.5	$\rightarrow 0$	−2.5	−2.5
0.30	6.6×10^{-3}	5.6×10^{-6}	−2.4	−2.4	7.2×10^{-6}	−2.4	−2.4
0.50	4.0×10^{-3}	2.6×10^{-5}	−2.4	−2.3	3.3×10^{-5}	−2.4	−2.3
1.0	2.0×10^{-3}	2.1×10^{-4}	−2.2	−1.9	2.8×10^{-4}	−2.1	−1.8
1.5	1.3×10^{-3}	7.3×10^{-4}	−1.9	−1.3	9.6×10^{-4}	−1.7	−0.9
2.0	1.0×10^{-3}	1.8×10^{-3}	−0.8	−0.3	2.4×10^{-3}	−0.3	−0.4
2.5	8×10^{-4}	3.8×10^{-3}	+0.2	+1.1	5.1×10^{-3}	+1.2	+2.3
3.0	7×10^{-4}	6.9×10^{-3}	+1.6	+2.9	9.7×10^{-3}	+3.2	+5.0
3.5	6×10^{-4}	1.2×10^{-2}	+3.5	+5.3	1.8×10^{-2}	+6.2	+9.2
4.0	5×10^{-4}	2.0×10^{-2}	+6.0	+8.5	3.1×10^{-2}	+11.1	+14.9
4.5	4×10^{-4}	3.3×10^{-2}	+9.7	+13.1	5.7×10^{-2}	+20.8	+26.5
4.8	4×10^{-2}	4.4×10^{-2}	+12.9	+16.9	4.1×10^{-2}	—	+2.7

further from the cornea as the pupil dilates and that the eye will become hypermetropic from the effects of spherical aberration. The eye will be in focus with a pupil approx. 2 mm in diameter. The effect of spherical aberration becomes more pronounced as the pupil diameter increases and at 4 mm the eye is between 6 D and 11 D hypermetropic.

The refractive states predicted by the model are in reasonable agreement with experiment. Hughes' (1977a) results are consistent with the view that the retinoscopic reflex arises at the vitreal retinal interface, rather than the outer limiting membrane which is the effective image shell (Glickstein and Millodot, 1970). This produces an apparent 8.9 D of hypermetropia (Millodot and Sivak, 1978; Hughes, 1979b). This model would predict an apparent hypermetropia with respect to the paraxial focal plane of the eye of 6.9 D which corresponds to an apparent hypermetropia of 9.4 D with respect to the effective image shell,

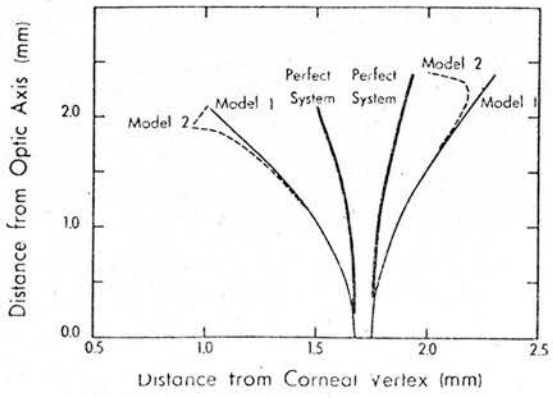

Fig. 11. The surfaces of unit magnification for a perfect system are spheres centred at the paraxial focal points. The more general surfaces of unit magnification for models 1 and 2 of the complete eye are shown here. They arise because of the presence of spherical aberration and coma. Close to the optic axis these surfaces are referred to as the principal planes. It can be seen that the paraxial treatment can be applied only within 0.5 mm of the optic axis.

Tables 2D, 2I. Hughes (1977a) found that the eye was nearly emmetropic within the 2 mm dia lens core and that it became rapidly hypermetropic at larger pupils. The model rat eye confirms that this results from spherical aberration.

Posterior nodal distance and retinal magnification factor

The nodal points are those on the optic axis at which the object and image points subtend equal angles. The displacement of the posterior nodal point from the focal image plane is the posterior nodal distance or PND.

From the value of the PND and the out of focus distance d. the retinal magnification factor, M, can be calculated in mm/deg for a small region of retina from $M = [2\pi(\text{PND} + d)]/360$, where (PND + d) is measured along the ray joining the nodal point and the image point. This differs from the definition of Vakkur *et al.* (1963) who employ the distance between the nodal point and the retina-choroid boundary, PND', as posterior nodal distance and set $M' = [2\pi(\text{PND}')]/360$. Because the retina-choroid boundary is not the effective image shell, their definition will give a slightly incorrect magnification factor.

Axial rays. The experimental PND value measured by transscleral illumination (Hughes, 1979a) will be equal to (PND + d + 0.03 mm.), Table 2C, if the viewed image measured is formed in the pigment layer (Hughes, 1979a). His experimental value of 3.39 ± 0.03 mm then corresponds to a magnification factor near the axis of 0.0586 ± 0.006 mm/deg. The paraxial retinal magnification factor suggested by the gradient index model is slightly smaller at 0.0571 mm/deg with a maximum value of 0.0574 mm/deg. The values for the core schematic eye are, before adjustment of the eye length to make the model emmetropic, 0.058 mm/deg and after adjustment of the eye to emmetropia, 0.0569 mm/deg.

Oblique rays. As the object and image points move away from the optic axis, the definitions of nodal

points, PND and magnification factor remain the same although their numerical values may change. The shape of the optimal image surface, aberrations and shifts of the nodal point along the optic axis could all cause changes in the PND and retinal magnification factor with eccentricity.

The nodal points of the model corresponding to a given obliquity were located by repeated ray traces. The incident position of a ray at a given angle of incidence was varied until the ray exiting from the system subtended the same angle; the results are given in Table 2G as a function of incident angle. Both models predict that the nodal point will be almost stationary with increasing eccentricity of the image point.

The position of the plane of best off-axis focus has not been measured but, as a first approximation, it might be assumed that the retina conforms to the best image plane. Hughes (1979a) measures a constant PND and a spherical retina of radius 3.09 mm for eccentricities up to 50°. A geometric construction shows this to be inconsistent with a fixed nodal point; either the retina is not spherical or the posterior nodal distance drops from the measured 3.39 mm to 3.27 mm at 50°. This 4% change might not be detected by the experimental technique employed. Alternately the posterior nodal point of the real eye may move towards the cornea faster than that of the model, giving a constant PND with increasing eccentricity.

Because of the finite field of view, the nodal points and posterior nodal distance cannot be defined at eccentricities greater than about 75°. Hughes (1979a) found indications that the retinal magnification factor decreases beyond 50°. A discussion of off-axis optics is required to determine the shape of the ideal image surface and the retinal shape requires accurate measurement.

Entrance and exit pupils

Several properties of dioptric imagery may be calculated from the image of the real pupil through the cornea—the entrance pupil—or its conjugate in image space—the exit pupil—which is the real pupil imaged through the lens.

In calculating *paraxial* properties, when either pupil may be used, the employment of the entrance pupil is usually preferable because the optics of the cornea can be defined more precisely than those of the non-homogeneous lens.

Diffraction limit. The diffraction pattern defines the ultimate potential resolution of optical systems and arises at the real pupil. The first zero of the diffraction pattern subtends an angle at the centre of the pupil,

$$\theta = \frac{0.61\,\lambda_{aqu}}{D_{pupil}} \tag{16}$$

Where λ_{aqu} is the wavelength of light in aqueous and D_{pupil} is the diameter of the real pupil. This is equivalent to an angle θ_1 subtended at the centre of the entrance pupil,

$$\theta_1 = \theta\left(\frac{n_{aqu}}{n_{air}}\right) \text{ (paraxial magnification factor of the cornea)}^{-1}$$

$$= \frac{0.61\,\lambda_{air}}{D_{entrance}} \tag{17}$$

where λ_{air} is the wavelength of light in air and $D_{entrance}$ is the *paraxial* diameter of the entrance pupil. The paraxial, non-aberrated, entrance pupil must be employed because a diffraction limited system is free of aberration in the image plane. This pupil may be calculated, as done by Hughes (1979a) for the rat, from the vergence formula of Bennett and Francis (1962). The position of the entrance pupil will however be behind that of the real pupil and the magnification factor, although remaining positive, will decrease slightly from that of Hughes (1979a). He treated the cornea as a thin lens where a thick lens approach is more accurate.

The paraxial entrance pupil and the ray trace entrance pupil, which is the observed pupil, differ because of corneal aberrations. The ray trace entrance pupil of even corrected dioptric systems may be influenced by corneal aberrations which are subsequently compensated for by the crystalline lens. This balance between corneal and lens aberrations occurs in the rat eye and has been hypothesized in man (El Hage and Berny, 1973), but is still controversial (Millodot and Sivak, 1979).

The spread of the diffraction pattern on the retina corresponding to the diffraction angle, θ_1 at the paraxial entrance pupil for a point source at infinity is $E' = \theta_1 f$ where f is the anterior focal length of the system. For a point source a distance x from the anterior principal plane and a distance y from the entrance pupil, $E' = \theta_1 fy/x$.

The deterioration of the diffraction image by aberrations may be computed by means of a complex Fraunhoffer integration (Born and Wolf, 1975). The region where diffraction is important to the rat has been qualitatively identified using the criterion of one quarter wavelength of spherical aberration. The Airy pattern widths may also be compared with the widths of the aberrated blur circles obtained from geometric optics (Welford, 1974), Table 2I. These two widths become comparable at an entrance pupil diameter of between 1.5 and 2.0 mm.

Illumination. The amount of light which enters an eye is proportional to the area of the *non-paraxial* entrance pupil. The diameter of an entrance pupil calculated for a perfect system is 3.16 mm but the maximum entrance pupil for a distant axial point is 3.0 mm, a 10% reduction in light gathered because of spherical aberration. For an axial object point closer to the cornea, the light entering the eye will depend on the numerical aperture of the system in object space. Because the rat eye displays spherical aberra-

tion and coma, and does not satisfy the sine conditions, the light accepted is not simply related to the numerical aperture in image space.

The illumination of the retinal image will depend on both pupil area and the inverse of the square of the magnification factor which varies as the distance from the posterior nodal point to the effective image shell. However, aberrations preclude perfect imagery of a point source and the resultant blur circle will reduce light concentration.

The illumination of off-axis points is reduced in the classic treatment by a factor of $(\cos)^4$ of the angle between the image principal ray and the optic axis (Born and Wolf, 1975). However, the reduction is only by a factor of $(\cos)^2$ of the angle when the focal surface is a sphere such as is approximated by the effective image shell. Variation of the magnification factor and the influence of higher order aberrations of the cornea on the entrance pupil will also influence off-axis illuminance.

The negative spherical aberration of the rat eye causes rays to be incident on the photoreceptors at shallower angles than in a perfect system of the same power and the Stiles–Crawford effect is thus reduced according to waveguide theory (Snyder and Pask, 1973). The 10% reduction in incident angle for the peripheral rays accepted by the fully dilated pupil means that they are more likely to be absorbed by photoreceptors than if the system were perfect or overcorrected for spherical aberration.

Exit pupil applications. A reference ray is required for consideration of factors such as local assymetries in an image or the optimal orientation of the photoreceptors for light capture. If magnification in the focal plane remains invariant with eccentricity of the image, then the ray which would pass through the centre of all pupils in a perfect system is employed—the principal ray of Born and Wolf (1975). Aberrations are measured with respect to the intersection of this ray with the effective image shell and photoreceptors are expected to be coaxial with it. If distortions cause the magnification in the effective image plane to vary with eccentricity then the reference ray should be taken as that which exits from the centre of a *non-paraxial* exit pupil. This ray is defined for each real pupil position by a ray trace through an infinitesimal pupil for a bundle at a given angle of incidence. The reference ray through the centre of the resulting exit pupil may not pass through the centre of the entrance pupil. If the magnification of the system is almost constant with eccentricity, the exit pupil may be estimated from a paraxial vergence formula analogous to that for the entrance pupil as calculated for the rat by Hughes (1979a). Unlike the calculation of Bennett and Francis (1962) the complete power of the lens, including that of the front surface must be employed. *Regardless of whether magnification is constant with eccentricity, a ray trace through a finite pupil* (rat: *Hughes, 1979a*, cat: *Vakkur and Bishop, 1963*) *is inappropriate.*

DISCUSSION

Design considerations

Physical constraints. The rat eye is small, which necessitates high power optics, and its nocturnal use favours a bright image. The maximum entrance pupil is relatively large and provides high light gathering power although its potential area is reduced by spherical aberration. The need for a large aperture precludes a small radius of corneal curvature so that the lens must contribute more dioptric power in order to ensure emmetropia. Siting of the lens to the rear of the eye reduces the posterior nodal distance, increases image brightness and imposes a requirement for additional lens power (Walls, 1942; Hughes, 1977b). In order to provide adequate power from the known range of physiological refractive indices, the lens must possess high surface curvatures or a steep gradient of refractive index. The former would minimize the equatorial diameter of the lens and reduce light capture, so it is understandable that the rat lens contains one of the steepest gradients of refractive index so far measured. The form of this gradient is important in controlling whole eye spherical aberration (Helmholtz, 1909).

Aberrations. The large gradient of refractive index within the lens reduces its spherical aberration from that of an equivalent homogeneous lens and drastically reduces the proportion of the eye's power contributed by the lens surfaces. Making these surfaces aspherical would affect spherical aberration little except near the equatorial regions. This contrasts with the human eye where the aspheric surfaces of the low power lens appear to be used for aberration control (Howcroft and Parker, 1977).

As suggested by Hughes (1979a), the cornea counters the spherical aberration of the rat lens and reduces that of the whole eye. A flattened cornea, as in man, would increase overall aberration and is not desirable. At the largest pupil the cornea reduces the spherical aberration of the eye by a factor of 8 from that of the crystalline lens alone.

Spherical aberration changes refractive state with pupil size. The model predicts a slight myopia at small pupils; the effective image shell may thus be conjugate with the hyperfocal surface and still be in focus for distant objects because of the eye's large depth of focus (Hughes, 1977a). The eye model will be emmetropic at larger pupils up to 2.5 mm dia and hypermetropic at fully dilated pupils.

Spherical aberration is substantial only when the rat pupil is large; under photopic conditions, however, the pupil diameter is less than 2.0 mm so that spherical aberration of one wavelength or less exists and the system is in focus with high optical quality. The pupil exceeds 2 mm dia only when the light levels are scotopic (Hughes, 1977b).

Linear coma, which produces a very assymetric image, is small and probably unimportant within the usual pupil range. The linear coma of the cornea and

lens are opposite in sign so that this aberration is dramatically reduced for the whole eye.

Projection of the visual world onto the retina. The rat eye is very symmetric and organised around nearly concentric and spherical sets of surfaces and isoindicial contours. Its nodal points are thus close to the centre of curvature of these surfaces and to the lens centre. If the system were completely concentric and spherical, the optical image quality and the magnification factor across the retina would be uniform apart from the small influences of pupil asymmetry. Because the rat visual axis is substantially eccentric to the optic axis, uniformity in the near periphery would not be surprising. The coincidence of the corneal and lens nodal points in the cat with the centre of curvature of the retina may imply a similar symmetry and uniformity near the optic axis of the cat (Vakkur and Bishop, 1963).

The nodal points are those on the optic axis about which a projection is made from object to image space. The indication of this model that the nodal points are almost stationary with increasing eccentricity is very important as the brief discussion of magnification factors showed. The nodal points in this schematic eye, and in most eyes for which they have been measured (see Hughes, 1977b, Table II), lie at or slightly posterior to the lens centre rather than more anterior in the eye. Thus the central region of the lens is used in the projection of the visual world onto the retina for all but the images on the extreme periphery of the retina. This allows for greater aberration control.

The specification of posterior nodal distance, retinal magnification factor and image quality as a function of incident angle is complicated by asymmetries such as are demonstrated in the departure of the surfaces from concentricity and the slight displacement of the nodal point from the centre of retinal curvature. Although not taken up here, a study of such off-axis properties is important for the treatment of peripheral imagery near the behavioural visual pole of the rat eye.

Schematic eye models

Experience with the gradient index eye enables the identification of several defects in previous models. A severe limitation in the majority of schematic eyes has been the use of a homogeneous lens. It generates excessively large spherical aberration and principal points which are farther apart than those of the crystalline lens. Even though a core model lens correctly estimates the position of the principal planes for the rat it would not necessarily be valid for other species or accurately predict spherical aberration. Schematic eye models obtained by fitting an arbitrary lens (core or homogeneous model) to a measured back vertex distance will only be valid for paraxial optics. As such, the lens models should be fitted to *paraxial* rather than finite pupil back vertex distances. This has not been done by earlier workers; in cat (Vakkur and Bishop, 1963), rabbit (Hughes, 1972) and rat (Hughes, 1979a) the back vertex power of the model lens was fitted to the position of a disc of least confusion. In the frog (Du Pont and De Groot, 1976) it was fitted to the average value of the inverse focal lengths measured at different ray incident heights. The error of these methods is proportional to the amount of lens spherical aberration.

Fitting the lens back vertex distance to a disc of least confusion might be expected to produce an eye model with a refractive state corresponding to that pupil size. However, in the rat core model eye, with a good approximation to the principal plane position, the refractive state is 5 D more hypermetropic than that of the gradient index model at the corresponding entrance pupil. This is because the paraxial equations used to combine the cornea and the lens are invalid at finite pupil sizes. If the rat core model (Hughes, 1979a) had been fitted paraxially, it would have accurately predicted the optics of the rat close to the axis.

The hypermetropic refractive state of the core model eye led Hughes (1979a) to provide a supplementary emmetropic model by increasing the axial length of the eye. This is not a unique change in the model and its limitations must be understood. Some of the ametropia in the core model arises from the systematic error in the method of calculation. Additionally, the presence of spherical aberration causes a change in refractive state with pupil size so that an ametropic, myopic eye at small pupils and a hypermetropic eye at large pupils is teleologically comprehensible. Depth of focus will minimize the effect of ametropia. The eye should not be adjusted to emmetropia for an arbitrary pupil size. When measuring refractive state the pupil size should be specified.

The usefulness of any model lies in its predictive powers. The development of the above model eye from anatomical and gradient index measurements is thus justified by its close agreement with the measured paraxial optics, spherical aberration, coma and refractive state. As demonstrated by the failure (Hughes, 1979b) of the rabbit schematic eye of Nakao *et al.* (1968), the final test of any model must be such agreement. But, alone, this may not be an adequate justification. A model which is highly sensitive to the exact value of its parameters has limited usefulness. Changes in the gradient of refractive index did not affect the qualitative results of this schematic eye. The sensitivity of the model to the isoindicial surface shapes remains to be determined. They have been assumed spherical in the foregoing discussion; any change in their shape may affect aberrations more than paraxial properties.

Acknowledgements—The authors would like to thank P. Donohue for technical assistance and C. Pask, P. McIntyre, P. Sands and A. W. Snyder for many helpful discussions.

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THE REFRACTIVE STATE OF THE EYE

Vision Res. Vol. 17, pp. 927 to 939. Pergamon Press 1977. Printed in Great Britain.

THE REFRACTIVE STATE OF THE RAT EYE

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(*Received* 26 *October* 1976)

Abstract—The retinoscopically determined refractive state of the rat eye is found to be 9D when the pupil is small. A calibrated fundus camera was employed for the differential ophthalmoscopy of the retinal surface vessels (+9D) and the choroidal vessels immediately subadjacent to the photoreceptors (−2D). Calculation from a rat schematic eye indicates the two refracted surfaces to lie +0.136 mm and −0.03 mm respectively from the plane of focus of the optical apparatus. This sets the plane of focus in the inner segments of the photoreceptors and indicates the rat eye to be close to emmetropic when the pupil is small. The identity of the retinal surface vessel and fibre refractions with that obtained retinoscopically confirms the hypothesis of Glickstein and Millodot in this species; a retinoscopic reflex originating at the vitread retinal surface gives rise to an artefactual appearance of hypermetropia in functionally emmetropic eyes.

Neurophysiological refraction of single unit receptive fields recorded from the optic nerve of the rat reveals considerable potential depth of field and is not inconsistent with an emmetropic state of the effective image shell when the pupil is small. Refraction by retinoscopy, optometry and neurophysiological assessment in the presence of a large pupil is consistent with some 6–10D of ametropia, in addition to the artefact of retinoscopy, which arises from aberrations of rays passing through the peripheral optical apparatus.

INTRODUCTION

The optical quality of the rat eye became of more than general interest when this animal began to be commonly used for behavioural experiments involving its visual capacities. Rat vision was declared poor as early as 1903 (Watson, 1903) and by 1912 a variety of observations, including the retinoscopic appearance of extreme hypermetropia in the wild animal, had been accumulated by Vincent in support of this view (Vincent, 1912). A revision of ideas on rat vision was subsequently called for when the introduction of the jumping stand enabled Lashley (1930) to reveal what he enthusiastically described as "a capacity of the rat to discriminate visual patterns which is little inferior to that of the primate".

The contents of Table 1 show that opinions on the refractive state of the rat eye have varied greatly; observations are recorded covering a total range of 30D, from 17D of hypermetropia to 13D of myopia.

The later results of Lashley (1930) indicate myopia of lesser degree than the 13D originally claimed (Lashley, 1932) but all of his observations were based upon the examination of scleral images in the excised eyes of albino rats and are subject to several possible sources of error, e.g. a spurious indication of myopia may occur if the image plane is within the sclera. Brown and Rojas (1965) and Partridge and Brown (1970) find the receptive fields of single retinal units to be smallest in size when plotted at a distance of 40 cm from the eye which suggests myopia of some 2.5D. This figure is said to agree with the plane of best focus determined with the retinoscope and with direct ophthalmoscopy on the retinal blood vessels but the finding is *impossible* because the blood vessels are considerably displaced from the plane of the photoreceptors at which the image is formed during the receptive field mapping technique. Montero, Brugge and Beitel (1968) are the only users of retinoscopy who claim the rat to be myopic (−3D) and of this, in view of the results subsequently presented, I have no explanation. In general, retinoscopy indicates hypermetropia exceeding 5D, most frequently of 10D, while Block (1969) describes equivocal reversal up to 20D.

Of these reports only that of Glickstein and Millodot (1970) specifies that some observations were made on animals with normal pupils, most of the published results, obtained after dilation with atropine, can have little relevance to the normal rat eye with its pupil constricted to a diameter of 1 mm or less under photopic conditions. Refraction with large pupils introduces the confusing effects of marginal ray aberration which may amount to as much as 3–7D even in man (Stine, 1930). Reinvestigation of the rat eye by retinoscopy thus appears called for.

In spite of an early account of the histology, optics and movements of the rat eye (Lashley, 1932) it was not until 1958 that a schematic eye was developed (Hermann, 1958) but this one was admittedly unsatisfactory. A consistent rat schematic eye was presented by Block (1969) with the conclusion that the rat eye is about 9D hypermetropic at the plane of the photoreceptors. Massof and Chang (1972) have recently questioned Block's methods but apparently concur that the rat eye is hypermetropic at the receptor plane. This conclusion is teleologically difficult to accept unless the small pupil offsets the effects of ametropia.

However, it is clear from other investigations (Hughes, 1977) that extraordinary accuracy of measurement is required if a schematic eye calculation is to be used to determine the refractive state of any small eye. The recent theoretically based suggestion that the retinoscopically observed hyper-

Table 1. Refractive state of the rat eye

Author	Date	Pupil		Refraction	Method
Johnson	1901	—	2–5D		Retinoscopy
Vincent	1912	—	+		—
Lashley	1932	—		−12 to −13D	Scleral image
	1937	—		−3D	Scleral image
Walls	1942	—	5–10D		Retinoscopy
Rochon-Duvigneaud	1943	—	+		—
Hermann	1958				
Brown *et. al.*	1965	Dilated		−2 to −2.8D	Retinoscopy Vessel ophthalmoscopy Unit field size
Siminoff *et al.*	1966	—	+		
Montero *et al.*	1968	Dilated		−3D	Slit retinoscopy
Block	1969	Dilated	9–20D		Retinoscopy
Glickstein *et al.*	1970	Normal Dilated	9D		Retinoscopy
Partridge *et al.*	1970	Dilated		−2.5D	Unit field size
Massof *et al.*	1972	Dilated	13–17D		Retinoscopy Ophthalmoscopy

metropia of small eyes is an artefact of method (Glickstein and Millodot, 1970) has made a definitive study of the refractive state of the rat eye essential. In the ensuing sections the problem has been tackled by comparison between the findings of retinoscopy, differential optometric refraction and the physiological refraction of the receptive fields of single units recorded from the optic nerve.

METHODS

Animal strain

The rats employed in this series of investigations were laboratory bred specimens of the D.A. (agouti) strain of *Rattus norvegicus*. Albino animals were not used because of their relatively lower proportion of uncrossed retinal ganglion cell axons (Lund, 1965) and inferior visual acuity (Lashley, 1938; Hermann, 1958). Transfer of the implications of this work to members of the wild rat population must be tentative until directly confirmed but it is worth noting that hooded, agouti and wild rats performed equally well in Hermann's acuity tests (1958).

Retinoscopy

All of the rats were refracted when lightly anaesthetised with urethane. Slit retinoscopy was begun at a working distance of 30 cm as soon as the animal became quiet after intraperitoneal injection of the anaesthetic. About 10–15 min intervened before the animal became incapable of spontaneous movement and retinoscopy was completed during this period. The image of the retinoscope streak could be readily seen in the majority of animals with a pupil about 1 mm dia. It was essential to keep the cornea moist with a saline drip for even this short period. Trial lenses were introduced in front of the eye, their posterior vertex separated by no more than 1 or 2 mm from the cornea, until a lens was discovered which induced reversal of the reflex movement. The refraction of the animal was taken as the power of this lens less an allowance of 3.3D for the working distance.

The refraction was also estimated by direct ophthalmoscopy; the necessary correction for a clear view of the retinal vessels and nerve fibres was noted. The bright corneal reflex of the ophthalmoscope light produced a defocussed image of constant size in the observer's field when his accommodation was at rest and enabled this factor to be controlled.

Optometric refraction

The Zeiss Fundus Camera incorporates an indirect ophthalmoscope of which the illuminating beam enters the eye through an annulus focussed in the pupil plane and the emergent beam is accepted by the instrument through the centre of the annulus. An image of the illuminated fundus is observed through a telescopic system which can accommodate −16 to 17D of refractive error in the range employed. The telescope eyepiece embodies cross hairs upon which the observer accommodated during focussing of the instrument and thus eliminates variations in the refractive state of his own eye.

The anaesthetised rat was mounted in a head holder and arranged so that dilated pupil of his atropinised eye was at the focal plane of the incident beam. A saline drip maintained corneal optical quality. The eyelids were retracted sufficiently to prevent the formation of a standing fluid lens on the cornea after a small cut had been made in the lateral canthus in order to avoid pressure on the globe.

The camera objective could be moved around the surface of a sphere centred on the pupil of the eye and thus used to examine various parts of the retinal surface. For the observation of a central ray bundle the minimum 2 mm exit pupil of the camera was reduced by a stop at the corneal plane to about 0.5 mm without significantly reducing the light entering the eye through the peripheral annular entrance pupil. As an alternative only a sector of the entrance and exit pupils was employed, a card stop being placed at the corneal vertex to block out the remainder. By raising and lowering the camera it was possible to arrange the unstopped, emergent beam sector so that it occupied the required portion of the pupil. The position employed for observing axial rays is shown in Fig. 1A and that for peripheral rays in Fig. 1B.

A model eye was calibrated by retinoscopy and accurately set to emmetropia. The model fundus was observed with the fundus camera and the telescope extension calibrated against lenses placed in contact with the vertex of the model eye lens.

Refraction was straightforward. Using the stopped down central ray bundle, the camera was focussed on the blood vessels and subsequently on the nerve fibres of the retinal surface—the position of best focus was readily established—photographic exposure was made and the extension of the telescope tube recorded so as to be later converted to a measurement of the refraction of the layer. The same procedure was then carried out for the deeper vessels of

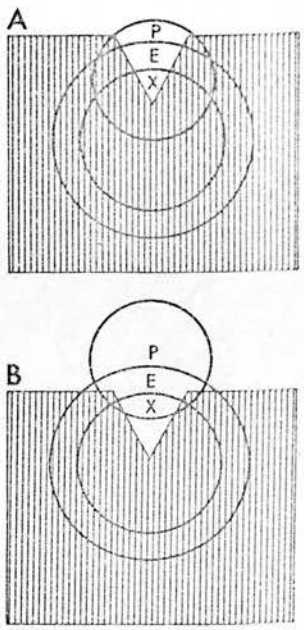

Fig. 1. The entrance, E, and exit, X, pupils established by the fundus camera were too large to enable separate sampling of central or peripheral ray bundles in the small pupil of the rat eye, P. A card stop, defined by the hatched region, bearing a notch was thus arranged to isolate a sector of the entrance and exit pupils so that rays leaving the eye in the exit pupil, X, passed through either the central region, A, or the peripheral region, B, of the dilated rat pupil, P.

the choroid or pigment layer which lie subadjacent to the plane of the photoreceptors. These vessels may readily be distinguished by their course which lies across the arteries and veins which radiate from the optic disc and by their colour which is orange rather than red.

The position of the telescope tube which gave a well defined image of the choroidal vessels was more difficult to establish than for the retinal surface features so the mean of the two extreme positions at which blurring was just apparent was recorded instead. A further photographic exposure was made and the process then repeated for a peripheral ray bundle. Four eyes have been examined in this fashion.

Neurophysiological refraction

Six D.A. rats of between 115 and 130 days of age were anaesthetised with an initial intraperitoneal injection of 1 cm^3 of 25% urethane solution. A tracheal cannula was fitted and the animal mounted in a head holder. The skull anterior to Bregma was opened on each side of the saggital sinus by means of a dental drill and the bridge of bone covering the sinus gently dissected away without rupturing the vessel. The sinus was ligatured and cut, the dura opened with a scalpel and the anterior forebrain and olfactory nerves removed by suction through a fine glass pipette to reveal the optic nerves in their course to the chiasm. The overlying blood vessels were left intact and a little paraffin introduced to prevent dehydration.

The animal was fitted with a rectal thermometer, wrapped in a homeothermic blanket and arranged facing a 1-m distant screen. The eyelids were retracted and a saline drip arranged to provide intermittent irrigation of the cornea. Single units were recorded by introducing 20-40 M/ohm NaCl filled micropipettes into the nerve by means of a Kopf hydraulic microdrive.

Visual stimuli were presented on the screen by means of a modified Keeler ophthalmoscope which produced slits or spots of light and a Leitz Prado projector fitted with a diaphragm and N.D. wedge. Card stimuli were available. Spectacle lenses from a trial case could be introduced in front of the eye at will but the arrangement of the head holder and the size of the lenses required that they be 20 mm from the eye so that magnification effects had to be taken into account.

The receptive fields were mapped out with a 30′ exploring spot of intensity 100 cd/m^2 against a background of 10 cd/m^2. The receptive fields of units evincing weak or non existent surrounds and sustained firing were alone explored. After the field had been localised the stimulus was moved into it along successive radii at intervals of 45° and the point at which firing began, in the case of an ON unit, and that at which maintained firing was inhibited, in the case of an OFF unit, was marked. The procedure was repeated several times on fresh plotting sheets after which the refractive state of the eye was changed by the introduction of a new lens on the axis of the receptive field and the plotting carried out again.

Under the conditions of plotting with the high background intensity and bright stimulus spot, it was found that the pupil remained very small, about 0.3 mm dia. Atropine was used to dilate the pupil in order to obtain a set of plots at a diameter of 4 mm.

RESULTS

Retinoscopy

The observation of reversal in the rat eye may be difficult for even experienced retinoscopists. It is essential that the cornea be kept moist because its optical quality deteriorates very rapidly if the eye is kept open without irrigation. *Given the small pupil*, it was found that reversal occurred over a quite narrow range of lens power, some 2–3D, and not over the range of 10D described by Block (1969). Of the 20 animals examined for this section, and of numerous examined routinely, none appeared to be less than 6D or more than 13D hypermetropic when refracted with a slit retinoscope. The mean refraction was 9.4D ± 1.83 S.D. (20); no animal was myopic. Direct ophthalmoscopy gave similar results; the mean of 15 refractions by this method was 8.0D.

Reversal was much more difficult to observe with a dilated pupil. A "scissors" movement in which two reflexes moved in opposite direction was usually present but an increase of the working distance to 50 cm and direction of attention to the centre of the pupil often enables a fairly clear reversal to be observed; this was achieved with lenses of similar power to those obtaining with a small pupil but higher power often eliminated the confusing "scissors" reflex. Such findings are characteristic of spherical aberration when observed in the human eye and may result from the entry of peripheral rays through the dilated pupil. It is likely that the anomalous range of reversal from 9 to 20D observed by Block (1969) is accounted for by the same factor because he made his observations on eyes with dilated pupils.

When the fundus reflex is examined through the dilated pupil it is possible to see the boundary of the lens core as a fine circular suture of about 1 mm radius centered on the optic axis. Rays entering the 1 mm wide annulus of lens cortex surrounding this

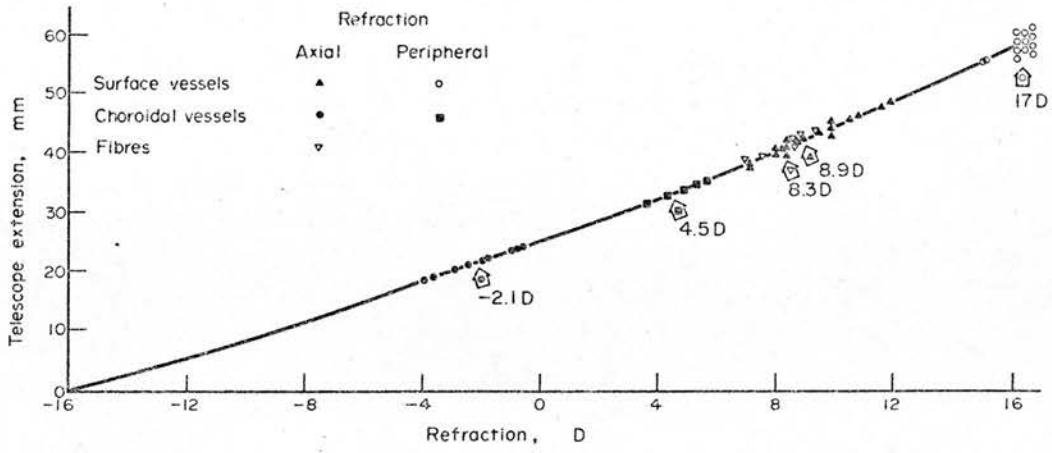

Fig. 4. Fundus camera calibration curve upon which are plotted the individual optometric refractions of the surface vessels, surface nerve fibres and choroidal vessels as determined by means of axial and peripheral ray bundles. The mean value of each group of readings is indicated by the arrow bearing the appropriate symbol. Change from axial to peripheral viewing increases the surface vessel refraction by 8.1D, from 8.9D to 17D, and the chorodial vessel refraction by 6.6D, from −2.1D to +4.5D.

do not pass through the lens core and may not be parfocal with the central bundle.

Optometric refraction

Photographs obtained by the fundus camera during optometric refraction with a beam some 10° above the optic axis are displayed in Fig. 2. The surface blood vessels and nerve fibres of the retina are sharply defined in set A_1, which corresponds to a refraction of 9.0D, while in set B, at a mean refraction of −1.5D, the nerve fibres of the surface are not visible and its blood vessels are blurred. The inverse is true for the choroidal vessels although the difference between the photographs is less marked.

The cup of this eye was dissected and photographed in order to positively identify the choroidal vessels. The photograph of Fig. 3A shows a region of the fundus near to the optic nerve head which includes the surface vessels shown in the fundus photographs A_1 and B_1 of Fig. 2. In spite of the deterioration of the optical transfer function of the dead retina it is possible to see the distorted outline of the same underlying choroidal vessels which are present in the fundus photographs of the living eye. After removal of the retina, Fig. 4B, it is easier to recognise the outline of the vessels and they are seen to lie in the pigment layer of the choroid.

The fundus camera calibration curve is shown in Fig. 4 with the values of extension used to observe the surface blood vessels, nerve fibre layer and choroidal vessels indicated for both axial and marginal ray bundles. The surface nerve fibres and blood vessels have very similar refractions of 8.25D and 8.9 ± 0.148 S.E.M. (20) respectively for axial ray observation; under the same conditions the choroidal vessels are located at a mean refraction of −2.1D ± 0.185D S.E.M. (9).

The mean refraction of the surface blood vessels was very similar through an exit pupil of 0.5 mm, 8.6D, or 2.0 mm, 9.0D, when viewed with an axial bundle close to the optic axis but, of course, avoiding the optic nerve head; it would appear that there is little spherical aberration for axial bundles of up to 2.0 mm dia, which is the largest beam that may pass through the lens core. We may thus accept the above values as the optometrically determined refractions of the respective layers.

Because the choroidal vessels are displaced from the focal plane of the eye by a distance equivalent to about −2.0D of power, it is only possible to conclude that the eye is close to emmetropia and that a pronounced myopia may be excluded because the photoreceptor layer is situated some distance in front of the choroidal vessels. The dimensions of the retina preclude the possibility of the photoreceptors being hypermetropic when 8.9D of power is required to view the surface vessels.

The results of measurements made along axes up to 45° nasal or temporal of the optic axis did not appear to differ significantly from those described above. Some measurements were made with the ray bundle entering the pupil on the horizontal but 60° nasal of the optic nerve head because of its importance both as the aperture for the region of most acute vision in the rat and as the area employed in binocular vision. In two animals the refraction of 5–6D for the surface vessels was less than that close to the optic axis; unfortunately no choroidal vessels could be observed. In frozen sections the retina is seen to reduce in thickness to about 2/3 of its central value in this region so that the reduced refraction of the surface is quantitatively compatible with emmetropic photoreceptors.

Refractions of the retinal surface vessels along limited marginal ray bundles parallel to the optic axis established the need for about 17D of power for a clear view rather than the 8.9D used for the limited axial bundle. Such power was required only when accepting light from an exit pupil near to the boundary of a fully dilated 4.0 mm pupil; these rays leave from the region of lens lacking core and comprised only of cortex. A similar increase in mean power to

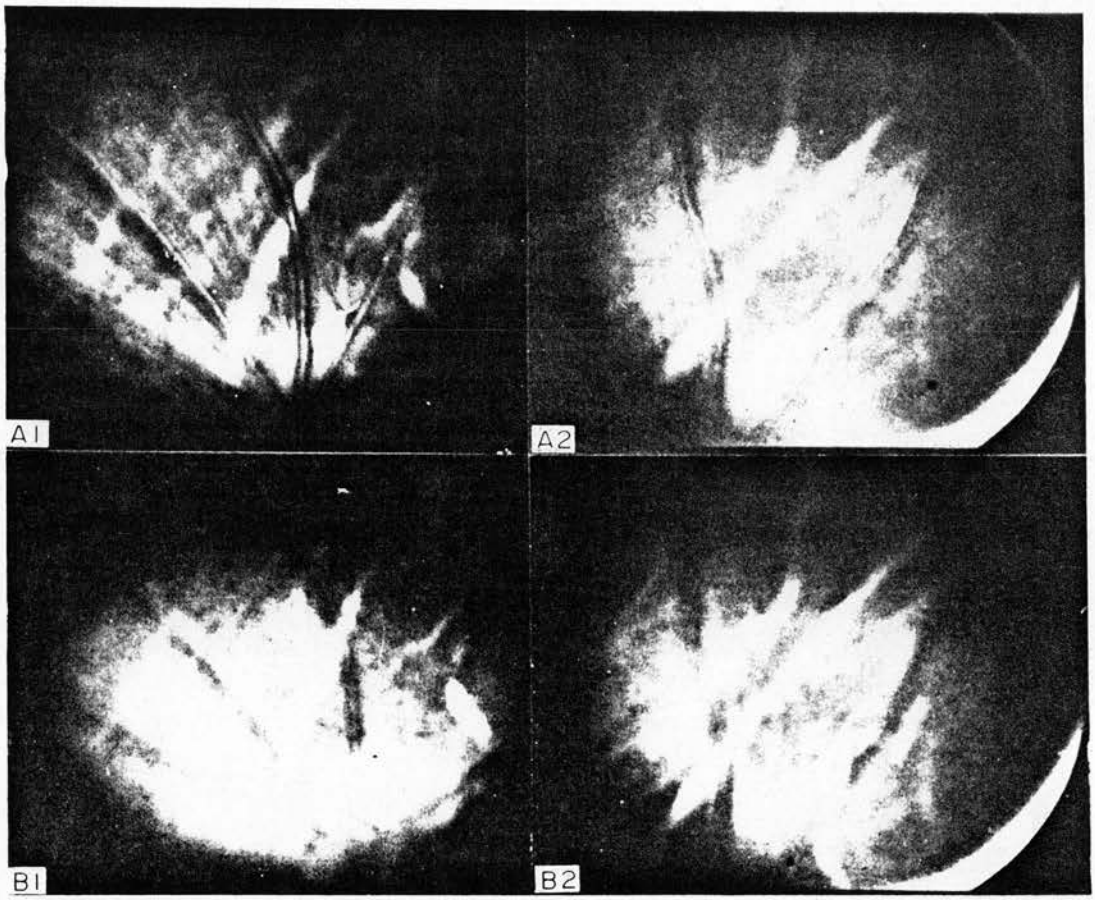

Fig. 2. Fundus camera photographs of the rat retina obtained with rays from a small axial bundle. In the photographs of set A the blood vessels of the retinal surface are clearly defined and in A_1 the surface fibres are also readily apparent; the blurred white lines which cross the blood vessels obviously do not radiate from the optic disc at the bottom centre of the photograph and underlie the surface vessels where they form the blood vessels of the choroid and pigment layers subadjacent to the retina. In set B the plane of focus has been changed from 9D to about −1.5D whereupon the surface vessels become blurred, the nerve fibres are no longer visible and the choroidal vessels become optimally defined although never as clear as the surface vessels. The choroidal vessels are situated in a plane close to the photoreceptor layer which indicates that this region must have a refractive state near to emmetropia. For details see text.

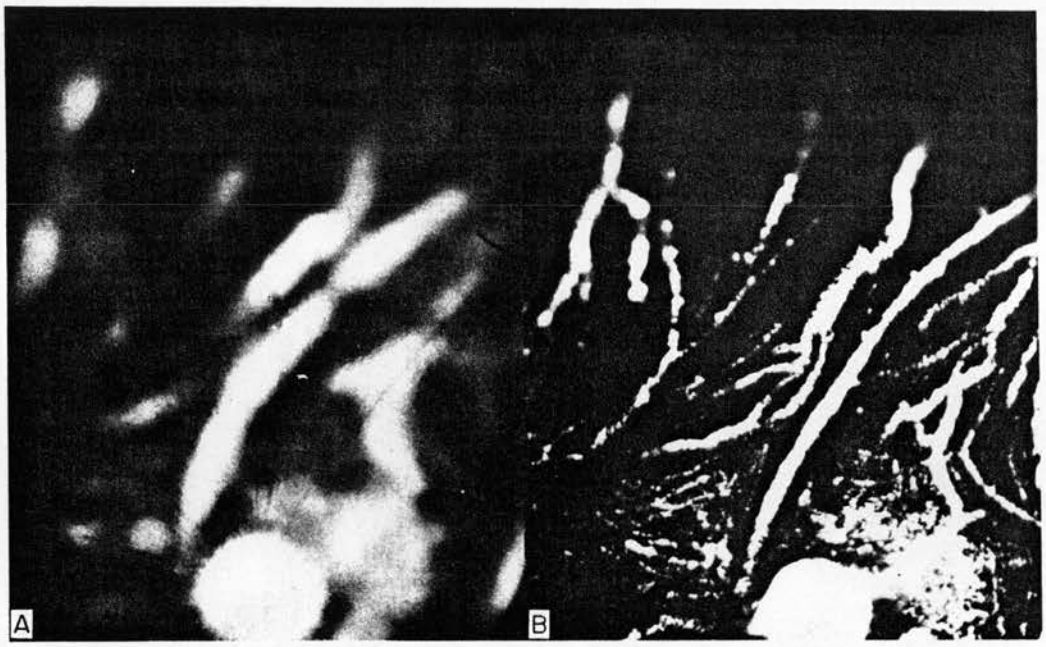

Fig. 3. Photographs of the opened cup of the eye whose fundus is illustrated in Fig. 3, A_1 and B_1, showing the appearance of the previously illustrated area by transmitted light when the retina is *in situ*, A, (the retinal MTF having deteriorated with enucleation) and after the removal of the retina, B. Vessels lying in the pigment layer subadjacent to the retina are seen in distorted outline in Fig. 4A and clearly in Fig. 4B from which they may be compared with and seen to be the same as those shown in Fig. 3, A_1 and B_1. The close anatomical juxtaposition of these vessels to the outer limiting membrane, the effective image shell, is used to argue the similarity of their refractions.

4.5D from −2.1D is required to view the choroidal vessels. The refraction of limited marginal beams, parallel to the optic axis, was determined in each quadrant of the pupil and found to vary in a given eye but even so, the minimum value was found to be 15D for the rear quadrant on one eye. These observations support the hypothesis of spherical aberration in the rat eye which was put forward earlier. In contrast to the situation in the majority of human eyes, although not in all, the rat appear to possess over-corrected rather than under-corrected aberration by virtue of the need of a positive lens for correction.

Neurophysiological refraction

The process of neurophysiological refraction consists of determining the optimal focus of an eye according to some arbitrary criterion related to the response of one of its single units and by recording from the optic nerve has the advantage of employing a living eye with undisturbed dioptric apparatus. It might be thought that mapping of receptive field boundaries with a small light spot according to a just audible response criterion would automatically lead to the identification of the focus at which the retinal blur circle and receptive field are smallest, but this is not necessarily true. Ikeda and Wright (1972) describe two classes of receptive field in the cat retina of which only one, that lacking a powerful surround, shows a change in size during defocussing. The dimensions of surround-dominated receptive fields do not show much change during defocussing although their response is reduced. It is fortunate that a class of receptive field possessing only a very weak, or no, surround is found in the rat (Brown and Major, 1965; Partridge and Brown, 1970) and may be employed to investigate the influence of focus, free from the complicating effects of surround.

After recording a sustained unit and locating its receptive field it was necessary to confirm the absence of a powerful surround before proceeding. This was done by examining the response to suprathreshold light spots ranging from 1° to 50° dia. In Fig. 5 is shown the response of the unit analysed below, Fig. 6, to a stimulus matched to its 2° receptive field diameter and to a 50° spot also centred on the field. The average number of spikes during the 5-sec light stimulus is slightly lower than for the 50° than for the 2° spot indicating only very mild inhibition from the surround; certainly not sufficient to lead to much error in the analysis.

The refractive state of the eye, K, was altered by placing appropriate lenses of power F at a distance c from the corneal vertex. Under these conditions the refractive state changes not by an amount equal to the power of the lens but by its effective power, F_e, at the cornea (Bennett and Francis, 1969) where

$$K = F_e = \frac{F_L}{1 - c \cdot F_L}. \tag{1}$$

A lens at some distance from the cornea has the additional effect that it changes the retinal image size, quite independent of blurring, by spectacle magnification, m (Bennett & Francis, 1969). The map of the receptive field in object space is thus subject to magnification which is the reciprocal of the spectacle magnification,

$$1/m = 1 - c \cdot F_L. \tag{2}$$

As uncorrected plot of effective lens power against receptive field diameter during defocussing is thus asymmetric about the value of added power for which the eye is emmetropic. Correction for spectacle magnification introduces symmetry by revealing the influence of blur circle size changes alone which are not a function of the sign of defocussing.

In a simple geometric treatment the blur circle diameter b, is given as,

$$b = \frac{e_x |d|}{E_x F' + |d|} \tag{3}$$

where e_x is the exit pupil diameter, $E_x F'$ the separation of the exit pupil plane from the posterior focal point and $|d|$ the modulus of the out-of-focus-distance for the given refractive error K. d may be obtained by arrangement from,

$$K = \frac{n_7}{A_1 A_8 - A_1 H'} - \frac{n_7}{H' F' + d} \tag{4}$$

(Hughes, 1977) where n_7 is the refractive index of vitreous, $A_1 A_8$ the separation of the corneal vertex from the effective image shell of the photoreceptor apertures, $A_1 H'$ the separation of the second principle point from the corneal vertex

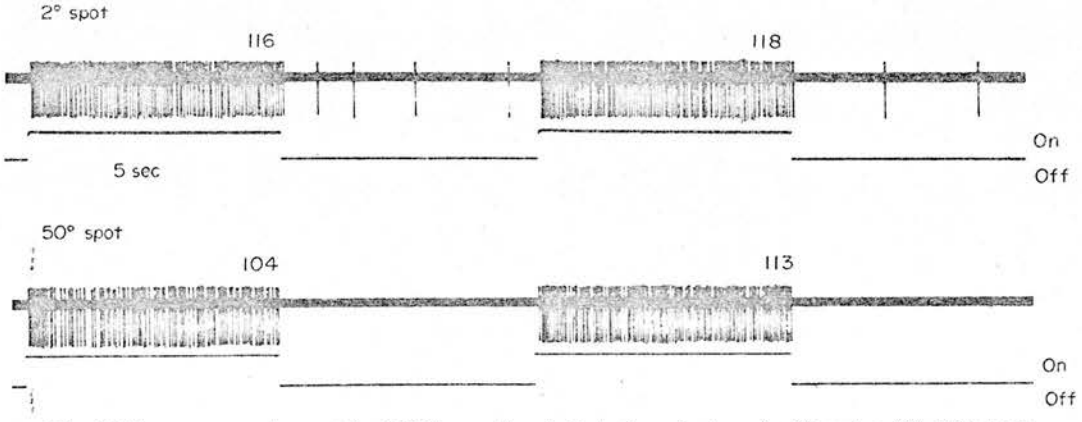

Fig. 5. The response of a sustained ON receptive field to 5 sec flashes of a 2° and a 50° light spot. The number of action potentials in the total 10 sec of stimulation shown is 234 in the first case and 217 in the second. The 7% reduction in the response and the inhibition of maintained firing during the OFF period when a 50° stimulus spot is centred on the field is attributed to the presence of a weak antagonistic surround which is neglected in the subsequent analysis. Intermediate stimulus diameters elicited no greater inhibition.

and $H'F$ the posterior focal distance. The angular diameter subtended at the anterior nodal point by a receptive field plotted with a point light source is thus equal to that subtended at the posterior nodal point by the summed diameter of the receptive field sensitivity profile and the blur circle for the given exit pupil diameter and refractive error, $b_{e_{x'},E}$. The minimum angular diameter of the receptive field is assumed to equal that of the sensitivity profile at emmetropia.

In fact the situation is much more complex and involves the convolution of the receptive field sensitivity profile with the pointspread function of the optical system at the given refractive state and pupil diameter. Such a treatment is not necessary for the following results. It suffices that the form of the receptive field diameter distribution changes in accord with the qualitative predictions of geometric optics.

During neurophysiological refraction it is best for the reliable detection of a change in refractive state between two pupil sizes that the same receptive field be employed. If both eyes are used and atropine applied to dilate the pupil then only two units may be examined in an acute experiment. Further restrictions were the requirements of obtaining the correct class of receptive field, of it being close to the optic axis and for it to be held for a sufficient duration that the experiment be completed. These difficulties resulted in only two units being completely refracted in the presence of both large and small pupils but the results were similar and in keeping with those for fields mapped with only a large or a small pupil.

In the absence of a spectacle lens and the presence of a 0.3-mm pupil the receptive field of Fig. 5 was found to be 2.1° dia. The observed receptive field diameters, both before and after correction for spectacle magnification, are shown in Fig. 6 for 0.3 and 4.0 mm pupils. The theoretical expectation of increased symmetry in the diameter distribution about the minimum value after correction for spectacle magnification is seen to be fulfilled.

The influence of defocussing on the receptive field diameter over the enormous range of refractive error investigated was negligible when the pupil was small; in addition, the minimum diameter of the field occurs in the absence of added power which indicates the eye to be emmetropic under these conditions as shown by the findings of optometric refraction.

After the application of atropine and dilation of the pupil to some 4 mm dia it is seen (Fig. 6), that the receptive field diameter changes substantially during defocussing. In addition the minimum value of its diameter was clearly shifted into the range of positive lens powers thus suggesting overt hypermetropia again in keeping with the findings of optometric refraction when peripheral ray bundles are employed. A plot of the theoretical receptive field diameter during defocussing, based on values from a rat schematic eye (Hughes, 1977), was made for the 4.0-mm pupil according to the above formulae. The deviations of the observed from the theoretical results are to be expected; the theory takes no account of any aberrations and thus indicates emmetropia at the minimum diameter and more pronounced blurring for a given refractive error.

While searching for units with receptive fields located close to the optic axis, the opportunity was taken to refract some of the randomly encountered

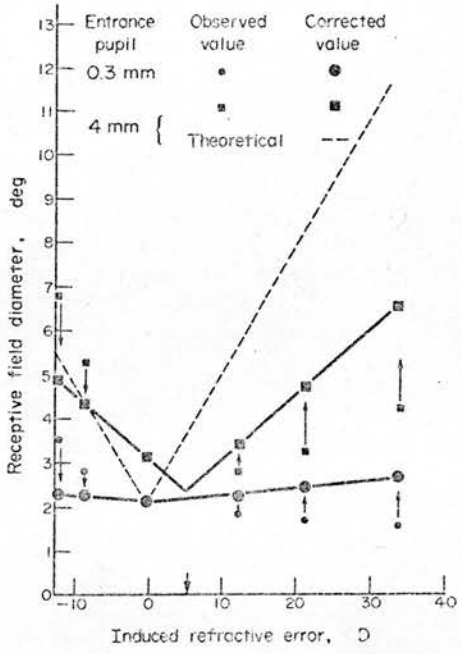

Fig. 6. The relationship between the plotted apparent receptive field diameter and induced refractive error for a receptive field lacking an antagonistic surround. Small discs and squares indicate the observed receptive field diameter for 0.3 and 4.0 mm pupils respectively. Arrows indicate the shift in receptive field diameter after correction for spectacle magnification effects; the corrected values are symbolised by large discs and squares. Theoretical calculation of the field size changes during defocussing by means of the equations given in the text are in close agreement with the corrected values for the 0.3 mm pupil. The theoretical predictions for the 4.0 mm pupil are shown as a dashed line under the assumption that the eye is emmetropic with a large pupil. The corrected observations fit as well as might be expected to the form of the curve derived from a very simple theoretical treatment but it is clear that the minimum field size is at about 6D suggestive of hypermetropia when the pupil is large. The technique is not accurate enough to put much reliance upon the apparent emmetropic minimum field size for the 0.3 mm pupil because the optical depth of field is so large. Optometric refraction suggests, however, that the eye is emmetropic when the pupil is small. It is thus concluded that hypermetropia appears as a result of aberrations revealed by the enlarged pupil.

units with receptive fields at varying degrees of obliquity. One set of such refractions was obtained while the pupil was small; after the pupil had been dilated during refraction of the selected central unit the search was continued until several obliquely situated fields had been refracted. The results obtained are shown for a few characteristic units in Fig. 7 after correction for spectacle magnification. Whatever the position of the receptive field, it was found that the influence of defocussing on its dimensions was very similar and fairly symmetrical about 10–12D of hypermetropia. This is larger than the ametropia suggested for the central unit analysed previously but that is not surprising as the major part of the ray bundle of obliquely situated units will be subjected to higher order aberrations. A systematic coverage

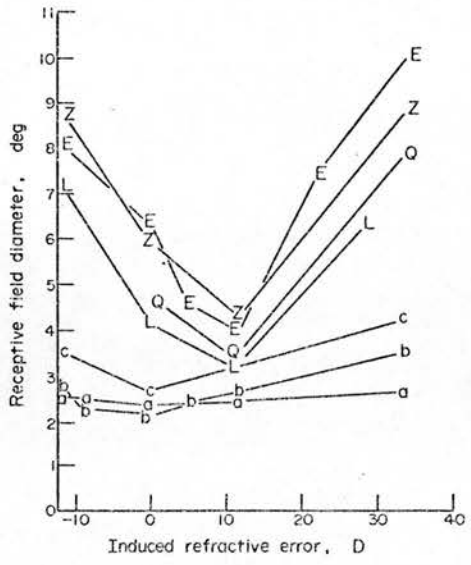

Fig. 7. The relationship between the apparent diameter of the receptive field and induced refractive error after correction for the effects of spectacle magnification. Lower case letters indicate observations obtained with a pupil of less than 0.5 mm dia; upper case letters indicate observations obtained when the pupil was fully dilated. Unit "a" was close to the optic axis, unit "b" 35° nasal of this on the horizontal, and unit "c" dead ahead on the horizontal. The influence of ametropia on the receptive field diameter is most evident for the unit "c" whose receptors receive non axial rays. If the pupil is small the receptive fields appear to be of minimum diameter when the eye is emmetropic although there can be no doubt of the presence of 10D of hypermetropia when it is fully dilated.

of the visual field was not attempted during these experiments but is does appear that the depth of field may be greatest for the central units when the pupil is small. In Fig. 7 are shown three units whose receptive fields were plotted when the pupil was 0.33 mm dia. All lay close to the horizontal but ranged from dead ahead to 90° temporal. These units suggest that the influence of defocussing on the receptive field dimensions is more pronounced the more obliquely rays enter the eye. The refractive anomalies of the oblique rays merit much more detailed examination because they are functionally of greater importance to the animal than those near to the optic axis; they are the rays which mediate both binocular and acute vision for the rate.

DISCUSSION

Retinoscopy thus suggests the rat to be hypermetropic to the extent of more than 9D. It has, however, long been known that in small eyes the separation of the plane of reflection used in retinoscopy from the photoreceptor plane may lead to the appearance of ametropia in functionally emmetropic eyes (Hirschberg, 1882; Beer, 1894).

Block (1969) uses such an explanation to account for the equivocal range of reversal from a "with" to an "against" movement in the retinoscopic reflex. He computes from his schematic eye that a shift in the plane of reflection from the vitread to the scleral retinal surface during retinoscopy is equivalent to a change in power of 10D. His conclusion is that the first sign of reversal of the reflex movement occurs at 9D with reflection from the photoreceptor plane and that complete reversal is obtained 10D later, at 20D, with reflection from the vitread surface. The photoreceptor plane is thus concluded to be 9D hypermetropic.

Glickstein and Millodot (1970) have recently demonstrated that the observed correlation between the magnitude of retinoscopinally determined hypermetropia and eye diameter would be expected if the reflex employed during retinoscopy arises at the vitread rather than the scleral retinal surface. Their conclusion that small retinoscopically hypermetropic eyes are functionally emmetropic has been shown to be valid for the frog (Moser, 1973) but is in conflict with Block's view that the photoreceptor layer in the rat is 9D hypermetropic. The foregoing observations enable this situation to be clarified.

The refractive state of the rat eye at the effective image shell

Small pupil. The results of neurophysiological refraction of the rat eye are such that they cannot be used to unequivocally establish its refractive state when the pupil is small; the presence of 6–10D of hypermetropia when the pupil is fully dilated allows of two interpretation. The eye may actually be hypermetropic regardless of pupil size, in accordance with previous claims in the literature, or this ametropia may simply result from aberrations introduced by the entry of peripheral rays in accordance with the indications of the previous sections on retinoscopy and optometry. The changes in receptive field size occurring during defocussing with a constricted pupil are so small that reliance could not be put upon the identification of the minimum diameter within an error equivalent to ± 5D.

The key observations for determining whether the eye is emmetropic with a small pupil must be those obtained from optometric refraction. The above results indicate the plane of the choroidal vessels to be refracted at -2.1 ± 0.185D S.E.M. (9) and the plane of the retinal surface vessels at 8.9 ± 0.148D S.E.M. (20) but do not have specific reference to the refraction of the effective photoreceptor plane. Inded, it is not clear from the literature where light should be regarded as coming to a focus in the normal eye accommodated to a given plane in object space. Given an accurate schematic eye it would obviously be straightforward to compare the plane of focus with the mean eye dimensions in order to establish this plane directly but in the rat an error of only 15 μm is equivalent of 1D in refraction and the accuracy of such models does not suffice. However, the optometric technique is highly accurate (S.E.M. $\pm$ 0.15D (20)) for the determination of *relative* planes which may be converted to distances by formulae which are quite insensitive to errors in the schematic absolute values. By rearrangement of equation (4) above and

substitution of values from the rat schematic eye (Hughes, 1977) we have,

$$d = \frac{n_7}{K - (n_7/A_1A_8 - A_1H')} + H'F'$$

$$= \frac{1.337 \times 10^3}{K - 300.7} + 4.446 \text{ mm.} \quad (5)$$

The −2.1D refraction of the choroidal vessels is thus determined to correspond with a plane 0.03 mm behind the effective image shell and the 8.9D refraction of the surface blood vessels to correspond with a plane 0.136 mm in front of it. What is its absolute position in the retina?

The choroidal vessels of the rat lie in pigment subadjacent to the retina and their borders are defined by gaps in the pigment at the retina/choroid boundary. The displacement from this layer to the vitread retinal surface is thus equivalent to the local retinal thickness and is optometrically determined to be 0.03+0.136 = 0.166 mm. From the rat schematic eye (Hughes, 1977) direct measurements on a sectioned eye and unfixed frozen sections are confirmatory in indicating the retinal thickness to be 0.17 mm. According to Lashley (1932) the outer and inner segments of the receptors total 40 μm in length and thus the outer limiting membrane is situated this distance vitread of the retina/choroid boundary; the emmetropic plane in optometric refraction is situated 30 μm from this boundary and thus appears to be halfway along the receptor inner segments.

For many years light has been commonly regarded as equally effective if in focus at any point along the axis of the photoreceptor outer segments; the extent of this region was suggested by Walls (1942) to increase the depth of field of the eye. More recently the concept of the photoreceptor as a "funneling" device indicates its aperture to be at the beginning of the inner segment (Baylor and Fettiplace, 1975) about which the organ appears to orientate (Enoch, 1972). Thus it has been suggested (Hughes, 1977) that the outer limiting membrane be regarded as defining a shell of image space, *the effective image shell*, at which light is brought to a focus during accommodation and subjective refraction. The above localisation of the emmetropic plane to the level of the inner segments of the rat eye is in substantial agreement with this suggestion.

This result is clearly in conflict with claims that the rat eye is *pronouncedly* hypermetropic or myopic when the pupil is small. A limited degree of individual ametropia is to be expected as a result of population variation and is indicated in the spread of the results of retinoscopy. Anatomical measurements probably introduce the main source of error into the above calculations and it is apparent that the mean refraction of the population at the effective image shell is somewhat ametropic; a slight degree of myopia could be argued to be advantageous in that an eye with its anterior focus at the hyperfocal distance may employ most efficiently any depth of field available. The presence of a great depth of field would reduce the importance of this benefit.

Large pupil. Neurophysiological refraction clearly indicates the presence of substantial hypermetropia for both axial and oblique rays when the pupil is fully dilated. The response of a unit to a flashing light spot accurately matched to the receptive field centre also peaks in an obvious fashion at some 10D of added power, thus confirming the presence of hypermetropia when the pupil is large. Optometric refraction through the peripheral pupil established the need for some 8D more power than required for axial refraction when observing both choroidal and surface vessels. The plane of best focus for an eye with a large pupil would thus lie somewhere between the focal points of the central emmetropic and peripheral hypermetropic rays. If aberration is significant only for rays which do not pass through the 2-mm dia lens core then, for a 4-mm pupil, these contribute 75% of the light incident on the retina and aberrant rays would thus tend to predominate in determining the *effective* plane of least confusion. It is of interest to note that the aberrant rays of the rat peripheral dioptric apparatus are overcorrected, not undercorrected as in man, and thus arise from the influence of the lens rather than the hemispherical cornea. The image degredation induced by such rays is minimised in man by the Stiles–Crawford effect (Campbell, 1957) but as this only occurs in cones it is unlikely to be of assistance to the rat at the low levels of illumination for which the pupil is fully dilated.

This explanation is quite compatible with the 11D range of retinoscopic reversal described by Block (1969) as encountered between 9D and 20D when refracting rats with dilated pupils. The initial reversal is that of the vitread retinal surface, not the photoreceptor plane as assumed by Block, and the 11D range is that during which the peripheral aberrant rays are brought forward from behind the retina and into focus on its vitread surface.

Does the rat eye have great depth of field?

It is obvious from the results of neurophysiological refraction that, when the pupil is small, substantial defocussing of the eye or any standing ametropia has little influence on the apparent dimensions of receptive fields close to the optic axis. It does not follow that the animal *must* have great depth of field. The problems involved in the definition of depth of field of an eye have been discussed in detail by Campbell (1957); it is clear that its assessment requires consideration not only of image quality but also of the resolving power of the neural apparatus alone. Depth of field, or the maintenance of visual resolution regardless of defocussing, is only possible when the minimum separabile of the optical apparatus is superior to that of the neural apparatus in the emmetropic eye. The behavioural minimum separabile for the rat has been established as 40′ (Lashley, 1938; Hermann, 1958). If this limit arose from neural factors alone in the presence of stigmatic imagery then we might employ geometric optics to compute a maximum possible depth of field for a given pupil size; it is only necessary to calculate the permissable axial displacement of a point image from the effective image shell before its blur circle becomes equal in diameter to the behavioural minimum separable and visual acuity reduced.

From the schematic eye of the rat (Hughes, 1977) we have the exit pupil diameter and position for a given entrance pupil size and by substitution in equa-

tion (3) above may determine the out of focus distance, and its equivalent in diopters, for a limiting 40′ dia blur circle. Geometric optics then suggests that, for a 0.3-mm pupil, a vergence change of some 64D would be possible before resolution suffered if the eye were emmetropic and the pointspread function of the rat dioptric apparatus of negligible width. The pointspread function of the rat eye has been estimated (Hughes and Wässle, 1977) to have a minimum width of some 13′ for a 0.3-mm pupil, and thus a similar optical minimum separabile, compared to the behavioural resolution of 40′. Allowance for the non-stigmatic emmetropic image in a geometrical model reduces the estimated depth of field for a 0.3-mm pupil from 64D to some 30D. This remains, however, exceedingly large in comparison with the human range of ±1.0D for a 1.0-mm dia pupil (Campbell, 1957). Any factor which tends to increase the pointspread function width will reduce the available depth of field and make the system more vulnerable to ametropia.

It is thus that, even for an ideal geometrical dioptric system, a large pupil of 4.0 mm dia would permit a range of only 2.5D of ray vergence before resolution is impaired; this corresponds a near point of 40 cm for an emmetropic rat eye. Realistic assumptions about the pointspread function and the presence of some 6–10D of hypermetropia indicate that the potential depth of field available to a small pupil must be absent when the pupil is large. The pointspread function is nearly 40′ dia for a 4-mm pupil (Hughes and Wässle, 1977) so that artificial dilation under photopic conditions might encroach upon resolution as well as eliminating depth of field. However, under natural conditions, the rat pupil diameter does not appear to exceed the diameter of the lens core until the illumination level is well into the scotopic range (Hughes, 1977) where it is probable that quantum limitations on resolution reduce or eliminate the significance of peripheral aberrations in restricting acuity.

The use of vision by the rat. The majority of those who have described the rat as ametropic appear to be satisfied with their respective estimates of its refractive error; discussion of the possible roles of accommodation and the stenopaeic pupil in ameliorating the effects of optical aberrations is only rarely encountered. The apparent inability of the rat to be trained in visual discrimination tasks (Vincent, 1912; Lashley, 1912) at first led to the attitude summarised by Walls (1942) when he said of the 5–10D of apparent hypermetropia that it, "Simply reflects the indifference of mice and mouse sized mammals in general to any refinements of vision relating to resolving power".

Block (1969) has suggested that Lashley, in claiming the rat to be myopic, was primarily concerned to show that the animals on his jumping stand were viewing the 20-cm distant stimuli under optimal conditions. He finds Lashley's comment, "the eyes are myopic and form clear images of objects within the more significant range of the animals activity," to be unsatisfactory because the rat has been shown to be guided more by the *distant* visual cues offered by the environment (Hebb, 1938; Lashley, 1938). Nearby objects are *not*, he alleges, the most significant for vision because, "at close range the rat has its nose and vibrissae to fall back on and only uses vision as a last resort" (Block, 1969). But this misrepresents Lashley who believed the rat eye to have considerable depth of field so that it, "forms fairly distinct images of even distant objects" (Lashley, 1930, 1932). However, according to Block's interpretation even such significant distant objects would, in the absence of accommodation, be subject to refractive errors in the order of 9D. Perhaps, like Lashley (1938) he believes, "That the rat's visual system functions most efficiently in spatial orientation—the recognition of relative distance and direction—and that identification of objects or forms, although possible, is secondary to a system of space coordinates", for such purposes the ametropic eye might be argued to function adequately whether hypermetropic or myopic.

In contrast to the views of these and other authors, there is ample literature available to suggest that the laboratory rat uses vision over quite a large range of depth and that it is not qualitatively different to that of "higher mammals". The visual environment of a maze is exploited by the rat as a source of visual clues to a greater extent than the maze itself. If it is of open or elevated construction (Hebb, 1938a, b, 1949, p. 42; Tolman and Honzik, 1930) features several meters away may be used by the animal for orientation. Carr (1917) found that rotation of a sideless maze increased errors eight-fold compared with the rotation of an enclosed maze but if the visual environment is rotated with the maze there is very little disturbance of performance (Higginson, 1917). The majority of enclosed mazes lack internal visual features and are run as efficiently by blind as by normal rats but even in this case Krechevsky (1933), Tsang (1934), and Lashley (1945) found an enormous range of visual dominance in the behaviour of individual rats and agree that the maze "dullards" are animals which depend upon the visual cues which are lacking in this form of test. The introduction of visual cues into the maze is accompanied by an increased rate of learning in sighted rats and their removal results in an increase in errors which reveals the reliance of the animal on vision in even the fully trained state (Honzik, 1936). Robinson and Weever (1930) also disclosed the ability to use perception of intra-maze cues in that rats could discriminate open from closed pathways at distances of up to 75 cm. in the conditions of their maze if pigmented but at only half this distance if albino.

The ability of rats to use their vision at close range is well established by Lashley's jumping stand experiments in which the animal views the stimuli at a distance between 30 and 25 cm. The claim that the rat, although possessing certain visual capabilities, does not resort to them when able to use his nose and whiskers (Block, 1969) may be true for certain rats in certain circumstances—e.g. maze bright rats in a closed maze—but has little evidence in its support as a general principle. Yoshioka (1930) has observed that both wild and laboratory rats in a lighted cubicle with free choice, thus not forced to use vision as in the jumping stand, will demonstrate a preference for a long sunflower seeds rather than short ones and that this disappears if they select their food in the dark. This discrimination is carried out at very short range—well within that of the vibrissae.

Does the rat accommodate? Accommodation or a great depth of field has in the past been regarded as redundant for an animal showing pronounced ametropia, which employs vision only for orientation to distant objects and preferentially uses its nose and whiskers for near work. However, it has now been demonstrated that the effective image shell of the rat is close to emmetropia under photopic conditions and argued that this species exploits both its distant and near visual environments over a range similar to that of other mammals. Emmetropia and the small pupil encountered under photopic conditions would appear to generate the potentiality for a depth of field substantially in excess of that of the human eye. The neural potentiality for a limiting resolution of some 40′ could thus be maintained over a wide range of depth without a specialised accommodatory mechanism. Under scotopic conditions the inevitable loss of optical quality consequent upon the expansion of the pupil must result in loss of that depth of field unless the capability for neural resolution also correspondingly deteriorates but it is to be emphasised that rat scotopic resolution need not decline so rapidly with reduction of intensity as in man because of the absence of a cone dominated area. An accommodatory mechanism might thus be redundant under photopic conditions but of advantage in mesopic or scotopic illumination to compensate for the development of the hypermetropia demonstrated in a previous section. The degree of advantage would depend upon the exact ratio in which the optical and neural factors influencing resolution undergo change with illumination and upon the manner in which the rat employs its vision.

The rat is usually said to be unable to accommodate (Tansley, 1965) but no conclusive evidence has been brought forward. Lashley (1932) assumed the poor development of the ciliary muscle to be indicative of the absence of accommodation and was unable to introduce change in the refractive state by electrical stimulation of the bulb. The stiffness of the lens, although a bar to deformative power changes, need not preclude accommodation because it could be achieved by translation of the lens; a shift of 0.15 mm would produce some 10D of accommodation.

Relevant behavioural observations. There is little behavioural material to be brought to bear on the above conclusions. What is available suggests that the rat possesses either a fair depth of field or some accommodative power. Both Lashley (1938) and Hermann (1958) were able to train rats to discriminate between gratings of 40–48′ *period* under photopic conditions of either diffuse daylight or illumination of 22 cd/m^2 respectively. However, Lashley's animals viewed the stimuli from a distance of some 20 cm and Hermann's from 40 to 95 cm without noticeable difference in performance thus indicating some 4D depth of field.

A recent behavioural study (Wiesenfeld and Branchek, 1976) has attempted to determine the refractive state of the rat by observing the influence of distance on its ability to resolve gratings of the same angular period. Most of the animals performed best at 30 cm viewing distance which is interpreted as signifying myopia. However, these rats at best resolved a grating of only 2° period which is substantially inferior to the results of Hermann and Lashley. Moreover, there are some curious anomalies in that equivalent drops in performance occur for steps of 5D of defocussing in one direction and 0.8D in another (e.g. rat, 7V) which suggests the presence of relevant variables not under control. These results are not in keeping with the findings of Lashley, Hermann or those presented above and require more detailed investigation before they can be accepted even for the strains examined.

Implication for retinoscopy in other species. Emmetropia at the effective image shell has been claimed for other retinoscopically hypermetropic species: pigeon (E.R.G. criterion; Millodot and Blough, 1971), frog (E.R.G. criterion Millodot, 1971; single unit refraction; Moser and Kruger, 1972; Moser, 1973) and fish (single unit resolution thresholds; Meyer and Schwassman, 1970). The cat is more problematic: Hill and Ikeda (1971) and Ikeda and Wright (1972) describe the cat eye as emmetropic after refracting single unit receptive fields; a technique involving averaged cortical evoked potentials confirmed this finding (Berkley and Watkins, 1973) but both sets of results are based upon animals fitted with contact lenses. In that the fundus reflex employed for retinoscopy of the cat is commonly regarded as originating at the highly reflective tapetum (e.g. Bonds, Enroth-Cugell and Pinto, 1972), it would be expected to reveal apparent myopia rather than hypermetropia in an emmetropic animal. The apparent hypermetropic refraction of the cat (Glickstein and Millodot, 1970) suggests overt ametropia, the involvement of dynamic accommodative mechanisms or a component of the reflex arising forward of the tapetum.

The results presented above for the rat supply the first direct demonstration that the retinoscopic reflex arises at the vitreous/retina interface as suggested by Glickstein and Millodot (1970). Millodot (1972) has computed that this layer provides 70% of the total reflected component during retinoscopy in man but this conclusion has previously been questioned because of Weale's claim (1966) that pigment bleaching changes both the specular and diffuse components of the reflex so that both must arise behind the photoreceptors. Weale's conclusion that the front surface component could not be significant is not borne out for the rat.

Results discordant with the suggestions of Glickstein and Millodot (1970) are limited. Sivak (1974) has claimed the schematically reconstructed refraction of the goldfish eye to be in keeping with a hypermetropic photoreceptor layer but 0.07 mm error in such small eyes amounts to 1D and accuracy beyond the capacity of the technique would be required to give credence to this view. Again Suthers and Wallis (1970) report only 10D of hypermetropia for the 1.68 mm long eye of the bat *Myotis* which calculation suggests should evince 65D of hypermetropia; in this instance, however, retinoscopy would be exceedingly difficult and possibly subject to considerable error.

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Vision Research, Vol. 18, pp. 1351–1355
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0042-6989/78/1001-1351$02.00/0

THE REFRACTIVE STATE OF THE RABBIT EYE: VARIATION WITH ECCENTRICITY AND CORRECTION FOR OBLIQUE ASTIGMATISM

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(*Received* 5 *December* 1977; *in revised form* 20 *January* 1978)

Abstract—A calibrated fundus camera was employed for the differential ophthalmoscopic refraction of rabbit retinal surface fibres (2.2D) and choroidal vessels (0.3D) immediately subadjacent to the photoreceptors; the effective image shell of this eye is thus within 0.6D of emmetropia. The retinoscopic and refractometrically determined axial refractive state of the rabbit eye was found to be some 2D of hypermetropia. The similar magnitude of optometric refractions of the surface fibres to those obtained by retinoscopy and refractometry confirms Glickstein and Millodot's hypothesis in this species; the retinoscopic reflex is thus dominated by rays originating at the vitread retinal surface and indicates an artefactual ametropia in emmetropic eyes.

Away from the optic axis, at eccentricities from −20° to 90°, the rabbit eye was found to remain within 1D of emmetropia on the visual steak; the frontal field was not found to be myopic. The tangential and sagittal image shells were coincident not only for axial but also for frontal rays. The rabbit eye is thus completely corrected for oblique astigmatism in the anterior field; this is consonant with its need to employ very oblique rays for imagery in the forward fixation area whose location is subsequent upon the lateral position of its eyes.

INTRODUCTION

A priori, it would be surprising to find substantial ametropia in the frontal field of short-distance cursorial species like the rabbit. However, De Graauw and Van Hof (1977) have recently reported the frontal refraction of the rabbit eye to be strongly myopic in contrast to the slight hypermetropia they observed on-axis. Their results are not in agreement with our own measurements, which are presented below.

It is important to realize that objective retinoscopy and refractometry do not necessarily define the refractive state of the behaviourally significant image shell located at the photoreceptor aperture plane (Glickstein and Millodot, 1970; Hughes, 1977a). This "effective image shell" (Hughes, 1977b) establishes the subjective refraction of the eye. In frog and rat the techniques of retinoscopy and parallax refractionometry measure the refractive state of the retina/vitreous boundary (Millodot, 1971; Hughes, 1977a) but their significance in the rabbit has not been established. We thus employed a Zeiss Fundus Camera for optometric refraction, indirect ophthalmoscopy with the observer's accommodation controlled, in order to measure the refractive state of specific retinal planes; these results were then compared with the findings of refractometry and retinoscopy. The method has previously been applied to the rat eye (Hughes, 1977a) and its theoretical basis recently outlined (Bengtsson and Krakau, 1977).

The lateral situation of the eyes in the rabbit ensures that the frontal binocular field is imaged on the extreme temporal retina. This region has a specialized ganglion cell distribution (Hughes, 1971), enjoys an expanded central representation (Thompson, Woolsey and Talbot, 1950; Hughes, 1971), and is employed as a forward fixation area (Van Hof and Lagers-van Haselen, 1973). Its situation, however, ensures that the image dealt with is formed by rays which pass obliquely through the optical apparatus. In an uncorrected optical system with spherical refracting surfaces and homogeneous media, such rays are subject to oblique astigmatism and eccentric refraction of the eye is a function of the orientation of refraction. The retina may lie either between the planes of focus or to one side of them (LeGrand, 1967; Millodot and Lamont, 1974); both arrangements occur in man. It thus does not suffice to specify the oblique refraction of a given species to be myopic or hypermetropic. A complete analysis should establish the plane of reflection and investigate the possible separation of the tangential and sagittal image shells by means of individual vertical and horizontal refractions. We employed a Hartinger refractometer to obtain separate vertical and horizontal refractions for the rabbit eye.

METHODS

A Zeiss Model Eye equipped with a 2 mm pupil was set to within 0.1D of emmetropia by means of slit retinoscopy. The model eye and a lens set were then employed to calibrate the focusing tube of a Zeiss Fundus Camera for use in optometric refraction; the image was brought to a focus in the plane of the ocular-crosshairs in order to ensure a constant state of accommodation in the observer. Tube extension was a linear function of lens power; the conversion factor of 1.75 mm/D is in good agreement with the theoretical value of 1.72 mm/D (Bengtsson and Krakau, 1977). Measurements of the refractive state of the model eye were repeatable within less than 0.25D. For the living rabbit eye a similar accuracy would be expected on-axis; at great eccentricities image quality is poorer and the plane of focus less easy to determine so that greater variability would be expected. A detailed description of the method has been given elsewhere (Hughes, 1977a).

Having centred the entrance and exit pupils of the fundus camera on the pupil of the eye, the observer brought into optimal focus either the visible detail of the pigment cell layer and choroidal vessels subadjacent to the photoreceptor layer or the bundles of nerve fibres on the retinal surface well below the optic nerve head and medullary rays. Surface fibres could not be distinguished in refraction of the temporal retina. Observations were made over 150° of eccentricity along the horizontal from temporal retina dealing with the binocular field to nasal retina dealing with the posterior field. The vertical range of observations was ± 5° and the measurements were thus concentrated along the visual streak.

The tangential and sagittal image planes were separately refracted from both lateral and frontal field with a Hartinger refractometer. The refractometer was checked against the calibrated model eye.

Measurements were made on four rabbits: Jane and Jenny were wild, sexually mature, 8-month-old animals weighing 1.3 kg; John was a pigmented laboratory rabbit of some 3 kg. For the measurements on tangential and sagittal image shells another laboratory animal, Justin, of the same weight was substituted for John. The animals, unrestrained for the duration of the observation, sat in the "freeze" position (Hughes, 1971). The intensity of illumination was adequate to maintain a small natural pupil about 3 mm wide thus minimizing peripheral aberrations.

RESULTS

The results of optometric refraction of specific retinal layers at various eccentricities along the visual streak are summarized in Fig. 1. The mean refraction of the choroid/pigment cell layer ranged from 0.0 to 0.6D of hypermetropia in the region of central visual streak which projects in the coronal plane below the optic axis. In the extreme nasal field the refraction of the streak increased to between 0.75 and 1.4D of hypermetropia; in the temporal field it ranged between 0.7 and 1.8D at some 45° eccentricity. The three solid lines connect the mean refraction of each animal at different eccentricities; the vertical bar indicates the S.E.M. and the number of measurements is noted below the bar. The dashed line connects the mean of the results from the three animals at major clusters of observations. The significance of the more oblique optometric readings is uncertain without the subsequent analysis because they are based on an estimate of focus which is a mean of rays in the vertical, horizontal and intermediate orientations.

The refractive plane of the surface nerve fibres as they pass through the visual streak below the optic nerve head was observed to be 2.0 and 2.3D, respectively, for two animals; this is in agreement with values obtained by slit retinoscopy close to the optic axis. Similar values were obtained with the means of the Hartinger refractionometer and are shown in Table 1 for central field. It is clear that axial retinoscopy and refractionometry refract a plane close to that of the surface fibres as defined by optometric refraction. In temporal retina the surface fibres could not be resolved.

The extent of oblique astigmatism was assessed by means of separate vertical and horizontal Hartinger refractions from both close to the optic axis and the

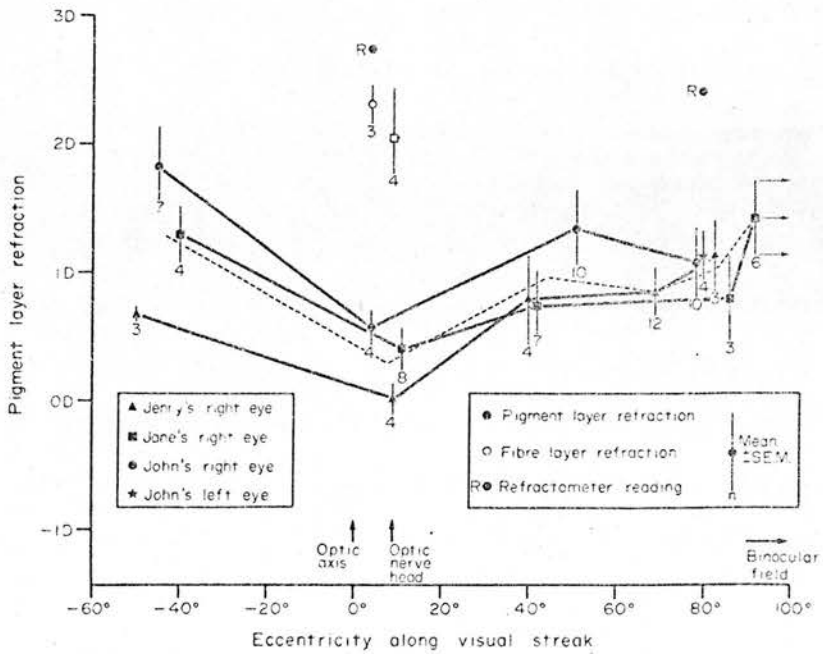

Fig. 1. Optometric refraction of the choroidal vessels adjacent to the pigment cell layer of the rabbit retina plotted as a function of eccentricity. Each point is the mean of several refractions at that eccentricity; the bar indicates the S.E.M. with the number of observations noted below. Measurements on three animals are plotted according to the inset key and joined by solid lines; the means of these observations at the major clusters are joined by dashed lines. It is apparent that over the range of eccentricity from −20° to 90° the mean refraction of this layer changes by less than 1D and that the photoreceptors of retina serving the binocular field must be within 1.1D of emmetropia. The axial refraction of the retinal surface fibres is indicated for two animals and the Hartinger refraction for one eye shown to demonstrate its similarity to the surface fibre optometric reading; the retinoscopic reflex is thus established as originating at the retinal surface. For more details see text and Table 1.

Table 1. Horizontal and vertical refractions of the axial and frontal fields of the left and right eyes of three rabbits

Animal	Eye	Refraction with Hartinger's refractometer (diopters) On-axis H	On-axis V	On-axis DIFF	Frontal field (90°) H	Frontal field (90°) V	Frontal field (90°) DIFF
Jane	L	1.7	2.2	−0.5	1.9	1.6	0.4
	R	1.9	1.9	0.0	1.3	1.9	−0.7
Jenny	L	2.0	2.1	−0.1	2.0	2.2	−0.2
	R	1.4	1.3	0.2	1.3	0.7	0.6
Justin	L	2.9	1.9	1.0	—	—	—
	R	2.2	3.1	−1.0	1.1	1.1	0.0
Mean		2.0 ± 0.5	2.1 ± 0.6	−0.1 ± 0.7	1.5 ± 0.4	1.5 ± 0.6	0.0 ± 0.5

The mean horizontal and vertical refractions are not significantly different at either eccentricity: thus the rabbit eye is corrected for oblique astigmatism. The lower value of the frontal field refraction is consistent with the known thinning of the retina in passing from central to temporal visual streak and shows the surface from which the reflex arises to be closer to the photoreceptor aperture plane in peripheral retina.

frontal field. Axial refractions were straightforward but refractions through the obliquely viewed pupil were more difficult because decentering could produce a change in the reading of up to 1D and reverse the sign of refraction. We found it necessary to plot the readings across the pupil; correct positioning was obtained in a small region of pupil within which the reading remained constant with slight paraxial shifts. The results for three rabbits are presented in Table 1. It is clear that the horizontal and vertical refractions are very similar to one another: their mean difference is zero and its standard deviation is 0.6D. The mean refraction on axis was 2.0D of hypermetropia but this decreased in the extreme nasal field to some 1.5D of hypermetropia.

DISCUSSION

Axial refraction

The refractometric and retinoscopic refractions of the rabbit visual streak below the optic axis indicate some 2D of hypermetropia in agreement with previous observations (Stone and Leary, 1957; Sorsby and Sheridan, 1953; Ludlam and Twarowski, 1973).

Optometric refraction of the same region of the visual streak showed the surface fibres of the retina to lie in the image shell requiring some 2.2D of extra power for its focus, whereas the choroidal vessels were close to the emmetropic image shell of the eye with a mean refraction of 0.3D for three animals.

We may convert the observed axial refractions into positions relative to the emmetropic image shell, or focal plane of the eye, by substituting values from the rabbit schematic eye (Hughes, 1972) into Eqn 1. This relates out-of-focus distance, d, to refractive error, K, (Hughes, 1977a).

$$d = n_7/(K + n_7/H'F') + H'F' \qquad (1)$$

where n_7 is the vitreous refractive index (1.337) and $H'F'$ is the separation of the second principal point from the second focal point (13.3 mm). Thus, from Fig. 1, we have

(a) Axial refraction of the choroid vessels, mean: 0.3D; −0.03 mm.

(b) Axial refraction of the surface fibres, mean: 2.2D; −0.28 mm.

(c) Axial Hartinger refraction, mean: 2.1D; −0.27 mm.

In this region of retina optical techniques thus indicate the separation of the choroidal vessel plane from that of the retinal surface fibres to be about 0.25 mm. After correction for some 25% shrinkage we estimate from Prince (1964) that the rabbit retina is 200 μm thick in the vicinity of the central visual streak. The choroid is some 30 μm thick in the living animal (Peregrine and Dodt, 1969) leading to an anatomical estimate of the maximum separation of the surface fibres from the choroidal vessels of 0.23 mm compared with the optically derived value of 0.25 mm.

According to the above measurements the emmetropic image shell would lie a further 0.03 mm behind the choroidal vessels. In this region of retina the length of the receptor inner and outer segments is about 40 μm (Prince, 1964) so that the photoreceptor entrance apertures would lie 0.3D vitread of the choroidal vessels, thus leading to a mean refraction of 0.6D for the effective image shell. Accommodative instability in the observer and depth-of-focus in the system would make this estimate not significantly different from emmetropia.

The on-axis results are thus in accordance with the prediction of Glickstein and Millodot (1970) that the effective image shell is close to emmetropia in spite of a retinoscopic or refractometric refraction of some 2D of hypermetropia. Similar conclusions have been reached for the frog (Millodot, 1971; Moser and Krueger, 1972) and the rat (Hughes, 1977a). The similarity between the Hartinger readings and the optometric refractions of the retinal surface fibres confirms, for the rabbit, Glickstein and Millodot's (1970) suggestion that the retinoscopic reflex originates at the retinal surface (Millodot, 1972); it has already been shown to be valid for the rat (Hughes, 1977a).

The mean optometric refraction of the choroid and pigment layer increases steadily to some 1D in the binocular field of the animal. The photoreceptor apertures will be only slightly more hypermetropic because the receptors of the temporal retina are short, with lengths equivalent to about 0.1D. These results are not consistent with the pronounced myopia reported by De Graauw and Van Hof (1977). In fact, *we have not obtained a myopic refraction at any*

eccentricity along the visual streak of the four animals studied. The effective image shell of the rabbit eye appears to be within 1D of emmetropia along the projection of the visual streak from the region of field 100° nasal of the optic axis to some 40° temporal. It should be noted that oblique refractions of the temporal retina from the binocular field are difficult; the S.E.M. of the readings increases and detail for accurate focusing is less apparent. It is possible that the effective image shell is nearer to emmetropia than the above readings suggest. Our findings are consistent with electrophysiological refraction of the rabbit eye which demonstrated (Meyer, Meyer-Hamme and Schaeffer, 1972) uniformity of the single unit *minimum visibile* from nasal to temporal field at presentation distance from 15 m to 40 cm. The *minimum visibile* did not deteriorate until lenses of power greater than 1D were introduced. These results are compatible with an eye close to emmetropia over a wide range of eccentricity, but certainly not with pronounced myopia.

Oblique refraction

As pointed out in the introduction, the significance of an oblique refraction must be assessed with care. Rays obliquely incident on the pupil may be considered as brought to focus in two perpendicular image shells: the tangential in the plane of eccentricity and the sagittal perpendicular to it. In a system of spherical refracting surfaces, these image shells will become more divergent at greater eccentricities; the retina may lie on either side of these image shells or between them. Alternatively the system may have aspheric surfaces or a non-homogeneous refractive index distribution so organized as to reduce "oblique astigmatism". The Hartinger refractometer provides a means of refracting the tangential and sagittal planes separately and hence of establishing whether the system is corrected for oblique astigmatism.

On-axis, as would be expected, the tangential and sagittal planes have similar refractions at some 2.0D (Table 1). The suprising observation is that this is also true for the frontal field at obliquities of some 80°–100°: the vertical and horizontal refractions of the retinal surface were both found to have a mean of 1.5D (Table 1). It follows that the vertical and horizontal refractions of the effective image shell will also be the same. *The necessary conclusion is that the rabbit eye is corrected for oblique astigmatism in the frontal field.* The interpretation of oblique optometric refractions is thus relatively straightforward.

The relationship of the oblique refractions to retinal anatomy cannot be dealt with quantitatively at present. The retinal thickness is substantially reduced in passing temporally along the streak until it reaches a value of some 120 μm in the region dealing with the binocular field. If the effective image shell in this region is emmetropic then the retinal surface refraction would be expected to be reduced relative to the central retina. Indeed this does occur in the Hartinger refractometer observations (Table 1). The 1.5D Hartinger surface refraction in the temporal retina suggests the less accurate optometric refraction of the choroidal vessels to be excessive at 1D. Their true refraction must be closer to emmetropia in order that the retinal thickness be accommodated between the focal planes. However, the actual refractive state of the photoreceptor apertures and choroidal vessels cannot be calculated from the oblique Hartinger surface refraction because Eqn 1 was developed only for axial optical systems and cannot be applied to oblique rays.

LeGrand (1967) calculates substantial oblique astigmatism for a model human eye with spherical refracting surfaces; at 45° the tangential and sagittal foci differ by some 8D in refraction. The refractions of Ferree, Rand and Hardy (Ferree and Rand, 1932) suggest that the retina in the majority of human eyes lies between the two image shells, or behind both, but the measured astigmatism was less than calculated. Their findings were subsequently confirmed by Millodot and Lamont (1974), who conclude that the crystalline lens, rather than the cornea, compensates for oblique astigmatism in man.

As a control for our methods we carried out horizontal and vertical refractions of three emmetropic human eyes at an eccentricity of some 45° temporal of the visual axis. A mean difference of some 4.5D was obtained between the two image shells with the tangential shell consistently myopic. This separation is similar to that reported by Millodot and Lamont (1974) but gross in comparison with the slight differences observed in individual rabbits at twice the eccentricity of measurement.

General

The reasons our findings on frontal refraction differ from those of De Graauw and Van Hof (1977) remains obscure. Their rabbits were refractometrically assessed as pronouncedly myopic on the basis of retinal surface reflections; the effective image shells must therefore be concluded to be even more myopic. We have noted that the ability to obtain rotation of the refractometer without change of refraction is dependant upon exact centering in the pupil. Peripheral aberrations of up to 2D could be obtained by off-centering the refractometer; these occasionally suggested myopia. The possibility that the retina lay between the tangential and sagittal image planes, as in man, and that De Graauw and Van Hof had refracted the tangential plane alone appears excluded, at least for our animal population, by the absence of oblique astigmatism. The hypermetropia of our laboratory bred animals suggests that the reported myopia is not an artifact of caging (Rose, Yinon and Belkin, 1974).

The extraordinarily well-developed visual streak of the rabbit retina (Hughes, 1971, 1977b) deals with nearly 180° of the visual field at a uniformally high ganglion cell density and it is consistent that peripheral aberrations should be minimized in the optical system serving such a retina. In addition, the lateral situation of the rabbit eye ensures that the temporal retina at an obliquity of some 80°–100° plays quite a different role to the equivalent region of the human eye. Its ganglion cell density distribution is specialized—the "anakatabatic area" (Hughes, 1977b); it contains the decussation line (Hughes, 1971); it has an expanded central representation; and it is employed by the animal as a fixation area. It is thus understandable that compensation for what would otherwise be very gross oblique astigmatism should be complete.

It is not clear which component of the optical system effects the correction but the peripheral cornea of the rabbit does appear to be somewhat flattened (Hughes, 1972) and may, in part, be responsible.

The results of this investigation suggest that the rabbit eye has up to about 0.5D of ametropia; its significance, if genuine, is difficult to judge. The rabbit eye does not have a small pupil and is thus unlikely to have a great depth of field; this has been electrophysiologically estimated as some 2D (Meyer *et al.*, 1972). It has been argued that the rabbit is incapable of accommodation because of the poor development of its ciliary muscles (Woolf, 1956). However, the literature does contain accounts of overt accommodation in rabbits (e.g. Olmsted and Morgan, 1941) and mechanisms involving the control of blood flow through highly vascularized tissues have been suggested (Prince, 1964). Neither we nor De Graauw and Van Hof (1977) observed variation in the refractive state of the conscious animal, but the recent description of change in vergence in the rabbit during close discrimination tasks (Collewijn and Zuidman, 1977) reinforces the belief that this species employs the temporal end of its visual streak for near, as well as distant, vision, and thus accommodation could be necessary.

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Vision Research Vol. 19. pp. 1293 to 1294
Pergamon Press Ltd 1979. Printed in Great Britain

LETTER TO THE EDITORS

THE ARTEFACT OF RETINOSCOPY IN THE RAT AND RABBIT EYE HAS ITS ORIGIN AT THE RETINA/VITREOUS INTERFACE RATHER THAN IN LONGITUDINAL CHROMATIC ABERRATION

(*Received* 29 *December* 1978)

Charman and Jennings (1976) concluded that the artefact of retinoscopy arises from the longitudinal chromatic aberration of the eye rather than by reflection at the retina/vitreous interface as suggested by Glickstein and Millodot (1970). Millodot and Sivak (1978) have since employed "chromoretinoscopy" (Bobier and Sivak, 1978) to establish that, although chromatic aberration is present in the eye of small animals it is of too small a magnitude to account for retinoscopic hypermetropia. More recently, Nuboer and Van Genderen-Takken (1978) have raised, yet again, the suggestion that chromatic aberration accounts for the artefact of retinoscopy in the rabbit eye. Employing a monochromater as a light source, they claim that retinoscopy reveals the rabbit to be about 1 D myopic with blue light and 1 D hypermetropic with red light. This result is in conflict with that of Millodot and Sivak (1978) who used Wratten filters to show the rabbit to be hypermetropic even during retinoscopy with blue light. The results of Nuboer and Van Genderen-Takken (1978) do not satisfactorily indicate why retinoscopy without filters leads to an estimate of 2.5 D of hypermetropia in the rabbit. The suggestion that red dominance in the reflex brings about this value is not compatible with their Fig. 4 in which it is apparent that even retinoscopy with infrared light at 750 nm would not achieve a value of +2.5 D. In view of these conflicting findings it was decided that reinvestigation of rabbit and rat refraction was required.

Both eyes of two rabbits and two rats with natural pupils were refracted by streak retinoscopy while the subject was under urethane anaesthesia. A working distance of 50 cm was employed and allowed for in calculating the apparent refraction. Retinoscopy was first carried out in the absence of a filter, then a bright spectrum blue (Ilford 622, 375–515 nm), tricolour red (Ilford 204; >610 nm) and, finally, a spectrum blue (Ilford 602, 440–490 nm) glass mounted filter successively interposed either on the animal's side of the retinoscope or between the retinoscope and the observer's eye. Some blue interference filters were also employed in the latter position when refracting the rabbit eye. The position of the filter was not important in determining the lens required to induce reversal of the reflex movement. The results are summarised in the Table 1.

The observed refractions are very similar to those of Millodot and Sivak (1978) and not compatible with the results of Nuboer and Van Genderen-Takken (1978). Retinoscopy with blue light brings neither rat nor rabbit near to myopia. In the rabbit this is true even when a narrowband interference filter is used in a double-pass arrangement which was precluded for the rat because of difficulty of observation. In both rat (Hughes, 1977) and rabbit (Hughes and Vaney, 1978) it has already been demonstrated that the effective image plane of the retina is nearly emmetropic and that the retinal thickness in the respective schematic eyes (Hughes, 1972; Hughes, 1979a) is just adequate to account for the artefact of retinoscopy if it arises by reflection at the retina/vitreous interface. The above chromoretinoscopic observations are compatible with these earlier findings if the chromatic aberration of the dioptric apparatus is understood as increasing or decreasing the retinal surface artefact.

In an accompanying note (Hughes, 1979b) a table of reduced schematic eyes including rat and rabbit has been presented which indicates the expected longitudinal chromatic aberration of a water filled reduced eye of each species. The *C–F* line aberration is presented above for comparison with the retinoscopic estimate of chromatic aberration.

Agreement between the simple model and the observations is good, as has been found for the human eye, but cannot be taken too seriously in the absence of more sophisticated model eyes. The basic qualitative finding of non-reversal of the artefact sign during retinoscopy with blue light is, however, substantiated.

Table 1. Mean retinoscopic hypermetropia in diopters (4 eyes; 10 observations each) for rat and rabbit. Values calculated from the reduced eye taken from Table 1 (Hughes, 1979b)

	No. Eyes	Without filter *D.*	Tricolour red. *D.*	602 Spectrum blue. *D.*	Chromatic aberration *D.*	Reduced eye chromatic aberration *D.*
Rats (230 gm)	4	+10.0	+10.5	+7.0	+3.5	+3.99
Rabbits (3.0 kg)	4	+3.0	+3.1	+1.8	+1.3	+1.34

Millodot and Sivak (1978) related their direct measurements of the chromatic aberration of an isolated rat crystalline lens at an unspecified pupil diameter to the rat schematic eye presented by Massof and Chang (1972) but the results of the latter have been criticised (Hughes, 1979a). The back vertex chromatic difference in power of the isolated rat lens was therefore incorporated into the homogeneous-lens model eye of Hughes (1979a) to calculate whole eye chromatic aberration. Values of dispersion for the ocular media and cornea were based on those of Nakao *et al.* (1968) for the rabbit media. This estimate was substantially larger than the retinoscopic results or reduced eye values. The eye was found to be 1.4 D hypermetropic for a shift from *D* line to *C* line light and 4.0 D myopic for a shift from *D* to *F* line light. The magnitude of computed hypermetropia still remains far from adequate to account for the +10 D artefact of retinoscopy in the rat and yet exceeds the observed aberration. In the rats and rabbits employed for this study it appears to be very unlikely that the artefact of retinoscopy arises in chromatic aberration rather than reflection at the retina/vitreous interface.

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Vision Res. Vol. 13, pp. 481-482. Pergamon Press 1973. Printed in Great Britain

RESEARCH NOTE

OBSERVING ACCOMMODATION IN THE CAT

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(*Received* 6 *June* 1972)

DURING a recent study of vergence in the cat (HUGHES, 1972) numerous photographs were made of the eyes of animals that were looking at objects either 10 or 100 cm distant. Illumination was provided by an electronic flash set on the horizontal and 20° lateral to the midline. It was noticed, in photographs of some of the animals looking at the distant stimulus, that a combination of shadow and displacement of iris markings delineated a bulging of the iris around the pupil within a circle of radius about 2 mm (Fig. 1a). The radius of this bulge increased as much as three-fold in photographs of the same cats looking at a 10 cm distant object (Fig. 1b). The bulge can be seen only when the pupil is relatively constricted but, within the range of sizes compatible with the observation, the variation of the pupil size appears to have no effect on its change of appearance in passing from a distant to a near look photograph. Under favourable conditions, side lighting and a relaxed, playful cat, the change may be directly observed; when an object is rapidly withdrawn from the animal's close observation into the distance the iris may appear to become completely flattened. Clearly these changes are linked with the process of accommodation. Similar forward bulging of the cat iris and lens during sympathetic stimulation was described by ARMALY (1959) but the phenomenon has not previously been described during voluntary accommodation in conscious cats. Direct evidence of accommodation in conscious restrained cats has, of course, been obtained by infra-red optometry (ELUL and MARCHIAFAVA, 1964).

The mechanism of accommodation in the cat has been uncertain since VAKKUR and BISHOP (1963) concluded from their schematic eye that a change in lens power would have only a minor effect on the refractive state of the cat eye. An alternative source of accommodative power was suggested to be the forward movement of the lens principle planes consequent upon either a change in the anterior surface curvature or the forward translation of the lens without change of shape. Any hypothesis of accommodatory mechanisms based upon a change of lens shape in the cat has been made unacceptable for mechanical reasons by FISHER's (1971) recent discovery of a very high value of Young's Modulus of polar elasticity for this animal relative to that of the human being. The forward bulging of the cat iris during accommodation and sympathetic stimulation must now be interpreted as resulting from lens translation and not from a change in surface curvature.

VAKKUR and BISHOP (1963) have described the pupillary margin of the iris as very thin and as lying closely applied to the anterior surface of the lens. The slight bulge in the distant-look photograph suggests that the remaining iris beyond 2 mm is not following

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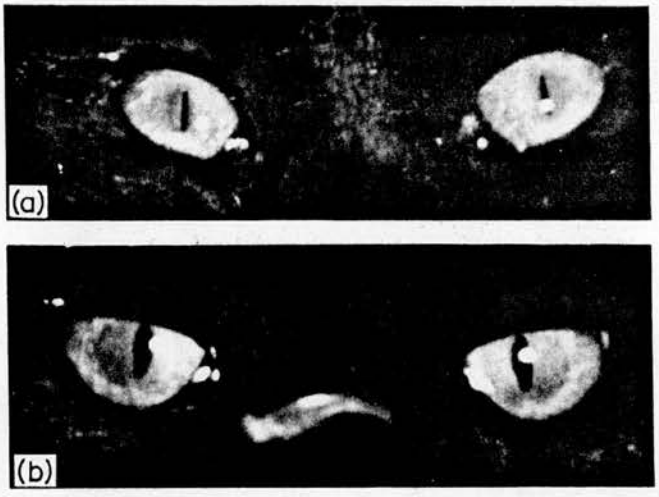

FIG. 1(a). The eyes of a cat that is looking at an object 100 cm away. Note the appearance of bulging of the iris adjacent to the pupil. This is not the result of pigmentation.

FIG. 1(b). The eyes of the same animal now looking at a 10-cm distant object. Note the nearly three-fold increase in the diameter of the bulge as indicated by shadowing and wrinkling of the peripheral iris.

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the lens anterior surface and only does so when the lens moves forward during accommodation.

If we regard the circumference of the bulge as defining the intersection of the iris and lens anterior surface then simple trigonometry now permits an estimate of the change in refractive power between the distant and near look photographs from measurements of the bulge radius. If the margin of the bulge remains in the same plane as it moves out from the visual axis then measurements of the bulge radius made on photographs at unit magnification must be corrected by the same value of corneal magnification; according to VAKKUR and BISHOP (1963) this would be 1·2 for the plane of the margin, which would nearly correspond with that of the lens anterior vertex in the emmetropic state. When R1 is the radius of the bulge margin corrected from a measurement on a distant look photograph, R2 is that for the near look photograph and the radius of curvature of the anterior surface of the lens is 7·2 mm (VAKKUR and BISHOP, 1963) then the forward movement of the lens, X, is given by,

$$X = \frac{R1}{\tan\left(\arcsin\ \frac{R1}{7{\cdot}2}\right)} - \frac{R2}{\tan\left(\arcsin\ \frac{R2}{7{\cdot}2}\right)}\ \text{mm}$$

which corresponds in the illustrated case to an increase in power of 3D, 0·8 mm forward movement, from an assumed 1D for 100 cm viewing distance to a consequent 4D for a 10-cm presentation distance. In view of the limited accommodation available to the cat (VAKKUR and BISHOP, 1963; ELUL and MARCHIFAVA, 1964) the discrepancy from the expected 10D is not improbable. This estimate of 0·8 mm for the forward translation of the lens in the conscious, voluntarily accommodating cat well exceeds the maximum value of 0·3 mm (1D) reported by O'NEILL and BRODKEY (1970) during ciliary ganglion stimulation in the anaesthetized animal.

With suitable animals the method provides a simple qualitative index of the presence of accommodation without the need for complex apparatus or excessive restraint of the cat.

Acknowledgment—I am indebted to the M.R.C. for support.

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GENERAL OPTICS

Reprinted from INVESTIGATIVE OPHTHALMOLOGY & VISUAL SCIENCE, St. Louis
Vol. 18, No. 8, Pages 878-881, August, 1979 (Printed in the U. S. A.)
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An estimate of image quality in the rat eye.

AUSTIN HUGHES AND HEINZ WÄSSLE.*

The point spread function on the optic axis of the rat eye is indirectly estimated to increase from a half-height width no greater than 12.5' to not less than 36' after dilation of a 0.33 mm pupil diameter to 3.0 mm.

A modulation transfer function (MTF) curve is not available for the rat. The following measurements provide an estimate of the *minimum* spatial frequency at which image contrast disappears close to the optic axis of the rat eye.

Methods. Observations were made on the eyes of five D.A. rats of between 115 and 130 days of age (215 to 230 gm weight). The animals were anesthetized by the intraperitoneal injection of 1 cc of 25% urethane solution and mounted in a head holder. Saline irrigation was employed instead of a contact lens. At first, the natural pupil was used, but later it was dilated by atropine. The apparatus of Fig. 1 is essentially that of Wässle.[1] A grating of transparent and opaque bands was

0146-0404/79/080878+04$00.40/0 © 1979 Assoc. for Res. in Vis. and Ophthal., Inc.

Volume 18
Number 8

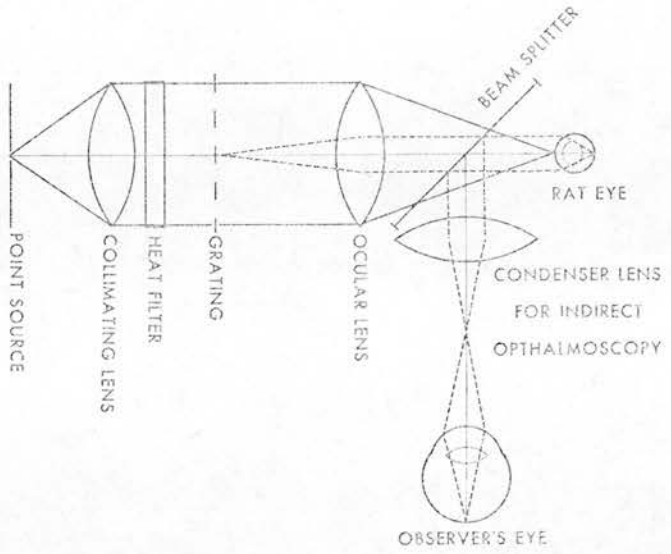

Fig. 1. Apparatus employed for the visual estimation of the double-pass spatial cut-off frequency of the rat optical system.

placed at the focus of a 110 mm camera lens (Super Takumar 55 mm; f2 plus APS Auto-Plus X 2), the ocular lens. The grating was illuminated by a collimating lens (Super Takumar 55 mm) with a pinhole source located at its focus. The necessary working distance and small pupil required the insertion of a 10 D lens at some distance in front of the observer's eye in order to increase the field of view by the use of indirect ophthalmoscopy. The living eye was centered on the optical axis of the system with the source in Maxwellian view. For a given size of pupil, the grating was introduced into the collimated beam and moved until judged in optimal focus on the retina. The effective frequency of the grating was increased by rotating it up to 45° about its vertical axis (defocus at edge <0.5 D); if the grating was still visible to the observer, then the process was repeated with a grating of higher spatial frequency until the contrast of the retinal image appeared to be just zero to the observer; this was sharply defined and taken as the *minimum* cut-off frequency.

Results. The visual angle subtended at the rat retina by the gratings was determined from a count of the number of cycles of the image which fell within the borders of the optic disc or between two vascular landmarks. The disc, or separation of the landmarks, was subsequently measured in the eyecup by means of a traveling microscope. The optic discs were very similar in size in different rats; in the animal discussed below, it was 0.384 mm across. Thus, because 0.059 mm on the retina subtends an angle of 1°,[2] the optic nerve head subtends 6.5° in the visual field. By inspection, four complete cycles of the image of a grating of 2.5 cycles/cm occupied the optic disc so that the spatial frequency of the retinal image of the grating was 0.615 cycles per degree (cpd). Frequencies expressed in grating cycles per centimeter may thus be converted to cpd in the retinal image by obtaining the product of the former with (0.615/2.5) = 0.246.

Over the period of an hour the natural pupil slowly changed size. The frequency at which grating contrast appeared to disappear in the retinal image was thus determined for three pupil diameters, 0.3, 1, and 2.5 mm, with the grating at the distance giving best focus on the retinal surface. This corresponded to about 8 or 9 D of extra power. The grating was also shifted to positions producing up to 8 D of defocus at each pupil diameter and the cut-off frequency for the defocused image again determined. The results of these observations are recorded in Table 1.

Discussion. The results thus indicate a spatial frequency of 3.8 cpd (15.6′ angular period) as the minimum frequency at which contrast disappears on axis in an emmetropic rat eye with a 0.33 mm pupil. Sampling theory leads to the expectation of local cone and ganglion cell densities at least matched to an optical image of this quality.[3] Although the above result necessarily underestimates the true value of the cut-off frequency because the rays make a double passage through the optics of the rat eye and the contrast sensitivity function of the observer has not been taken into

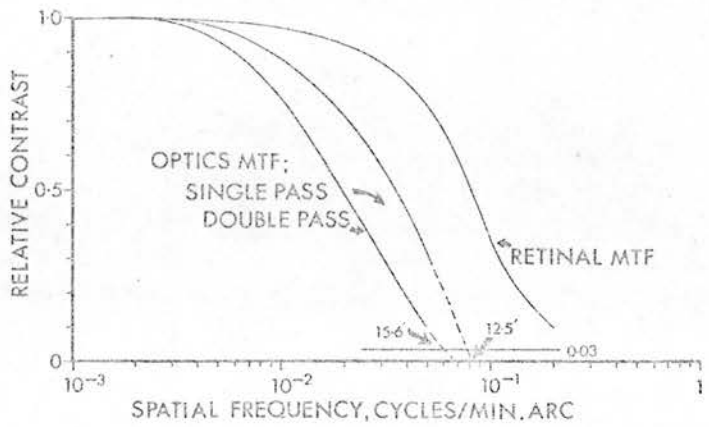

Fig. 2. Krueger and Moser[8] have shown the form of the optical MTF to be very similar for different species of vertebrate eye. In the absence of a rat MTF we have positioned the double-and single-pass MTF profiles obtained for the cat by Wässle[1] to approximately represent the situation for a rat eye with a 0.33 mm pupil. Assuming a 0.03 modulation threshold for the observer (not critical, see text), the double-pass profile has been arranged so that a 15.6′ cut-off period just reaches the modulation threshold. The extrapolation of the single-pass MTF to the abscissa then indicates a single-pass cut-off period of 12.5′. The MTF obtained for the isolated rat retina by Ohzu et al.[9] lies well above the estimated optical MTF and suggests that the overall MTF for optics and retina, as determined at the photoreceptor apertures, would be little different to that for a single passage to the retinal surface.

Table I

Pupil diameter (mm)	*Defocus relative to retinal surface (D)*	*Observed at cut-off*		*Nomographically computed single-pass angular period at cut-off (min arc)*
		Grating frequency (cycles/cm)	*Double-pass angular period (min arc)*	
Rat 1:				
1/3 mm	0.0	15.6	15.6	12.5
	8.0	13.0	18.7	14.9
1.0 mm	0.0	14.1	17.2	14.0
	8.0	11.7	20.8	16.7
2.5 mm	0.0	10.0	24.3	19.3
	8.0	7.3	33.3	26.4
Rat 2:				
1/3 mm	0.0	14.9	16.3	13.0
1 mm	0.0	13.0	18.7	15.0
Rat 3:				
1/3 mm	0.0	14.3	17.0	13.9
Rat 4:				
3 mm	0.0	5.9	41.2	36.0

account, the cut-off value is already of interest because it is substantially better than the cut-off frequency calculated from either cone density, 1.86 cpd, or ganglion cell density, 2.3 cpd[3] and exceeds the optimum behaviorally determined phototopic resolution of 1.5 cpd.[4, 5] The central region of the observer's pupil intersected the entire emergent beam at the smaller rat pupil diameters with the condensing lens and viewing distance employed. When the rat pupil was fully dilated, however, the performance of the rat optical system may be overestimated in Table I. The marginal rays of the rat pupil which pass through the marginal region of the observer's pupil have their efficacy reduced by the Stiles-Crawford effect, so that marginal aberations which occur in the second pass through the rat optics will be underestimated by the observer. We thus consider only the small pupil data.

With assumptions we can assess the possible

underestimation of the true cut-off frequency resulting from the double pass when the rat pupil is small. The influence of equipment MTF would be negligible. For a rat eye of posterior nodal distance (PND) 3.4 mm,[2] a 10 D condensing lens, and an observer viewing the real image of the emmetropic fundus from a distance of 33 cm, we calculate[6] the grating image in the observer's eyes to be about 13 cpd at cut-off. The observer's modulation threshold in this region would lie between 0.1 and 0.01,[7] and the properties of his visual system would not substantially influence the apparent cut-off frequency of the rat optical system. Krueger and Moser[8] have shown the MTFs of a variety of species to be very similar in form, so we assume the shape of the cat single-passage MTF[1] for the rat (Fig. 2) and compute the double-passage MTF as its square (Fig. 2). Assuming 0.03 for the observer's modulation threshold, the double-passage transform is set to intersect this modulation at the observed cut-off frequency, and the extrapolation of the single pass transform to the abscissa is read to obtain the minimum estimate of the single pass cut-off frequency. Estimates of this value have been included in Table I as well as data for other sizes of pupil and focus. Choice of between 0.1 to 0.01 for the modulation threshold varies the cut-off period from about 10′ to 13′, indicating the most probable range of the true cut-off period. In practice, this may be roughly equated with the half-height width of its inverse transform, the point spread function (PSF).[3] It can be seen from Fig. 2 that the retinal MTF for the rat[9] is substantially better than the single-pass optical MTF estimate, and a cut-off measured at the level of the photoreceptor apertures would differ little from that at the retinal surface.

Optical resolution close to the optic axis as estimated from the single-pass cut-off according to the Sparrow criterion[3] is thus about 12′, which is considerably better than Lashley's[10] value of 30′ obtained by transcleral imagery at an unknown pupil size. His value would be consistent with a fully dilated pupil according to Table I. The great depth of field of the rat eye established by single unit refraction[11, 12] results directly from the narrowness of the PSF relative to the ganglion cell receptive field sensitivity profiles when the pupil is small, and the above results are consistent with the literature. Pupil diameters from 0.33 to 1.0 mm are common in the rat under photopic conditions and small enough for diffraction effects to be significant. For yellow light Airy's disc is 7.5′ diameter with a 0.33 mm entrance pupil, clearly outside the above range for minimum PSF width. It thus seems unlikely that more accurate measurements will show the image quality to be completely diffraction-limited; for a 1.0 mm pupil, Airy's disc is 2.5′ diameter and not significant in relation to the estimated 15′ single-pass PSF half-height width. The great obliquity of the fixation axis precludes assessment of the role of diffraction in limiting behavioral resolution.

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Key words: rat eye, point spread function, modulation transfer function, optical quality

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Vision Research Vol. 21, pp. 955 to 956, 1981
Printed in Great Britain

0042-6989/81/060955-02$02.00/0
Pergamon Press Ltd

TECHNICAL NOTE

CONTACT LENSES CHANGE THE PROJECTION OF VISUAL FIELD ONTO RABBIT PERIPHERAL RETINA

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(*Received* 8 *December* 1980)

With the exception of Choudhury (1978), previous studies of rabbit binocular cortex have employed contact lenses to prevent drying of the cornea. Bishop *et al.* (1962) established that a contact lens increases the posterior nodal distance of the cat eye and changes the projection of the visual field onto retina. It appeared possible that the application of a contact lens to the peripheral binocular optics of the rabbit might introduce significant error when mapping the projection of binocular cortex into the visual field and measuring the disparities of binocular units. Without an estimate of the magnitude of the effect it remained possible that the remarkable 20° divergent disparities reported for rabbit binocular units (Van Sluyters and Stewart, 1974) could have their origin in this artefact.

Eyes were enucleated, supported in a cup, and punctured with a fine hypodermic needle at the superior pole. The needle was connected to a saline reservoir and the pressure of the posterior chamber maintained at 18.7 mm Hg, (Gökhan and Gokçe, 1975). The posterior ciliary vessels were set horizontal, the boundary between the cornea and sclera vertical, and the optic nerve head projecting 9° forward of the 0° vertical meridan. This is equivalent to the "freeze" position of the rabbit eye (Hughes, 1971).

Miniature lamps were set in front of the eye at the 90°, 80°, 72°, 64°, 46° and 36° meridia, and formed images visible transclerally through a travelling microscope positioned to the rear, Fig. 1. The horizontal shift in the image of each lamp was measured when a contact lens was put on or taken off. The eye did not move between measurements as shown by scleral landmark stability. One eye from each of 7 rabbits weighing between 2.5 and 3.5 kg was tested and the shift in the image of each lamp measured 3 times before conversion to angular representation.

Application of the contact lens caused the image of the lamp centred on the 90° meridian to shift laterally by some 0.38 mm (2.3°) towards the retinal margin. The image of the lamp 26° eccentric on the 64° meridian shifted peripherally by some 0.10 mm (0.63°). Although the results showed substantial individual variation, Fig. 2, the mean shift decreased with increasing eccentricity from the 90° meridian, was not a function of the rabbit's weight over the range tested and was not influenced by a 25% variation in intraocular pressure. The regression line for the mean shift, $\Delta X°$, as a function of eccentricity from the 90° meridian, $X°$, was

$$\Delta X° = 0.0627\ X° - 2.42°$$

for a range of 25°. Movement towards the temporal margin of the retina is taken as a negative shift. Outside the range of 25° the shift becomes progressively smaller and is zero at the 36° meridian, Fig. 1.

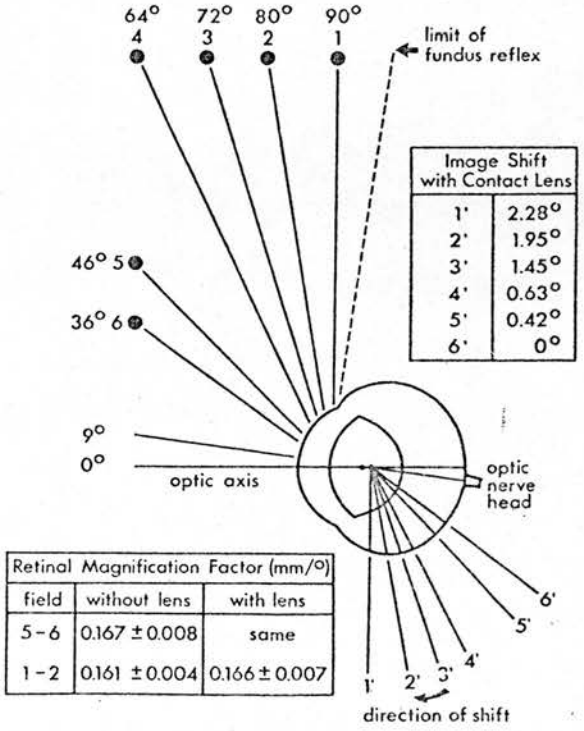

Image Shift with Contact Lens	
1'	2.28°
2'	1.95°
3'	1.45°
4'	0.63°
5'	0.42°
6'	0°

Retinal Magnification Factor (mm/°)		
field	without lens	with lens
5–6	0.167 ± 0.008	same
1–2	0.161 ± 0.004	0.166 ± 0.007

Fig. 1. Shift in the retinal image upon application of a contact lens. The projection of the shifted image is shown for six points in the horizontal plane with azimuths ranging from 36° to 90° nasal of the optic axis. The tables show the angular magnitude of the image shift and the retinal magnification factors at various eccentricities.

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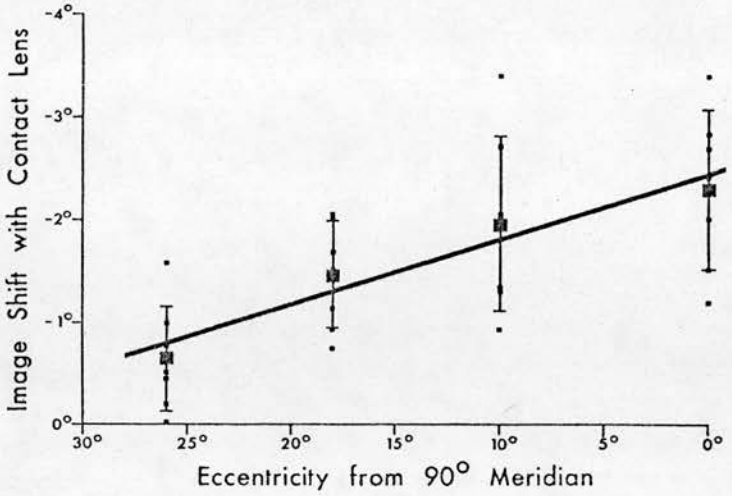

Fig. 2. The shift of the transcleral image along the horizontal plane when a contact lens is applied is plotted as a function of object eccentricity from the midline. Small squares indicate individual measurements; large squares indicate the mean shift for six eyes; vertical lines indicate 1 SD.

In the absence of a contact lens, the magnification factor for central retina (within 30° of the optic nerve head) was 0.167 ± 008 mm/deg; in binocular retina it was smaller at 0.161 ± 0.004 mm/deg. These values are similar to those of Hughes (1972) for central retina (0.17 mm/deg) and temporal retina (0.15 mm/deg). The contact lens did not alter the central retinal magnification factor, but did increase that of binocular retina by 3% to 0.166 ± 0.007 mm/deg. These values are thus significantly different from the 0.20 mm/deg reported by Barlow and Levick (1965) for a rabbit eye fitted with a contact lens.

Application of a contact lens should thus shift the projection of a point on binocular retina to a position in the visual field more eccentric from the midline. During a cortical mapping experiment, the small image shift measured in the enucleated eyes could be demonstrated physiologically by plotting changes in the projection of receptive fields on a tangent screen. The projection of the electrophysiologically defined visual I/II border into the visual field was located some 7° from the midline on an animal prepared and set up without contact lenses in order to avoid possible corneal deformation. Application of a contact lens caused the projection of this decussation line to be shifted some 2.5° further from the midline. This shift is comparable in magnitude to that seen optically in the equivalent region of the enucleated eyes.

The shift in projection of rabbit binocular field upon application of a contact lens is thus in the correct direction to produce apparent divergent disparities between binocular unit receptive fields but not large enough to account for their reported 20° magnitude. This problem is taken up elsewhere (Vaney and Hughes, 1979; Hughes and Vaney, 1981). Those concerned with topographic mapping of field imaged by peripheral optics in rabbits and other species should clearly adopt procedures which eliminate the need for contact lenses (Choudhury, 1978) or at least calibrate them and correct for their influence.

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